DIETS, DISTRIBUTION AND POPULATION DYNAMICS OF ARCTIC COD (*BOREOGADUS SAIDA*) IN ARCTIC SHELF ECOSYSTEMS

By

Jennifer M. Marsh

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APPROVED:

Franz Mueter, Committee Chair
Seth Danielson, Committee Member
Katrin Iken, Committee Member
Terrance J. Quinn II, Committee Member
Milo Adkison, Chair
Department of Fisheries
S. Bradley Moran, Dean
College of Fisheries and Ocean Sciences
Michael Castellini,
Dean of the Graduate School

Abstract

With climate warming and longer open-water seasons in the Arctic, there is an increased interest in shipping, oil exploration and the expansion or development of commercial fisheries. Anticipated natural and anthropogenic changes are expected to alter the Arctic shelf ecosystems, including their fish communities. As a component of the Arctic Ecosystem Integrated Survey (Arctic Eis), this project presented a unique opportunity to assess the ontogenetic, spatial and temporal variability in the distribution, abundance and trophic roles (trophic level and diet sources) of key fish species in the Chukchi Sea. For my dissertation, I addressed three objectives to advance our understanding of Arctic cod (*Boreogadus saida*) as a key component of Arctic ecosystems. First, I characterized the current range of variability in trophic roles within the system and explored the role of advection in shaping the fish communities' diet (isotopic signatures) with a focus on Arctic cod. Second, I examined environmental and biological influences on the distribution and abundance of Arctic cod and provided an updated stock assessment for the Chukchi Sea. Finally, I broadened the geographic scope and used available time series of survey data at the southern margin of their range in the Pacific (eastern Bering Sea) and Atlantic (Newfoundland/Labrador shelves) sectors to assess the influence of temperature, predators and competitors on their distribution. Compared to age-1+ Arctic cod, age-0 Arctic cod had a less diverse diet regardless of water mass and were limited to colder temperatures. Together, this suggests that younger Arctic cod are more vulnerable to climate change. Estimates of egg production and early survival suggest that the numbers of mature Arctic cod present in the survey area during summer are unlikely to produce the observed high abundances of age-0 Arctic cod in the Chukchi Sea. Moreover, Arctic cod distributions in their southern ranges were highly influenced by temperature and to a lesser extent by competitors and predators. When temperatures were warmer, Arctic cod occupied a smaller area. These results inform the management of Arctic cod in a rapidly changing environment and provide benchmarks against which to assess future changes.

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General Introduction

Arctic cod have been consistently identified as the most abundant forage fish throughout the Arctic (Lowry and Frost 1981; Barber et al. 1997; Beniot et al. 2008; Rand and Logerwell 2011; Logerwell et al. 2015, 2018; David et al. 2016; De Robertis et al. 2017). As such, they provide an important ecosystem role linking plankton to apex predators and transferring energy between benthic and pelagic communities (Welch et al. 1992). Many migrating seabirds (Matley et al. 2012), marine mammals (Lowry et al. 1980; Laidre and Heide Jørgensen 2005; Bluhm and Gradinger 2008) and some fish species (Lilly 1991; Bowering and Lilly 1992; Yaragina and Dolgov 2009; ICES 2012) rely on Artic cod for prey, as they are abundant and have high energy density (Harter et al. 2013). In addition, Arctic cod are targeted in subsistence (e.g. Magdanz et al. 2010) and commercial fisheries (Gjøsæter 1995). Arctic cod are considered generalist zooplanktivores, but their diets vary by region and have demonstrated adaptability in dynamic environments (Bradstreet et al. 1986; Coyle et al. 1997; Cui et al. 2012; Gray et al. 2016).

Despite their ecological importance, there is relatively little information on the stock structure of Arctic cod throughout their circumpolar Arctic range. Genetic studies have found low, but significant genetic differentiation between regions across the Arctic (Nelson and Bouchard 2013; Madsen et al. 2016). Notably, across the Artic three groupings (western, central and eastern) were found based on genetic heterogeneity, which correspond with geography (Nelson and Bouchard 2013). Additionally, population differentiation was found across the north Bering-Chukchi-Beaufort-Amundsen Gulf corridor with Amundsen Gulf and Tuktoyaktuk samples being differentiated from US samples (Nelson and Bouchard 2013). No genetic population structuring was found in the US Chukchi and Beaufort Seas suggesting that Arctic cod in the US Arctic are a single panmictic population (Nelson and Bouchard 2013; Wilson et al. 2017). In the northeast Atlantic, population differentiation was observed between Arctic cod inhabiting individual fjords and shelf habitat, possibly due to reproductive isolation (Madsen et al. 2016). In the fall mature Arctic cod migrate from their summer feeding grounds to spawn in the winter (November to March), typically under ice (Ponomarenko 1968; 2000). Few spawning areas have been confirmed, but are suspected to occur throughout Arctic shelves (Ponomarenko 1968; Craig et al. 1982;). Spawning sites have been identified in the Barents Sea: east of

Svalbard (inferred from egg and larval drift (Hop and Gjosaester 2013) and Pechora Sea (Rass 1968). Historically, the only managed stock of Arctic cod is in the Barents Sea, which biomass has been estimated through acoustic surveys since 1986 (ICES 2012).

Due to extreme seasonality and freezing temperatures in the Arctic, few fish species inhabit the Arctic year round. Arctic cod are adapted for sub-zero temperatures (Osuga and Feeney 1978) and low-light conditions (Jonsson et al. 2014). In many regions Arctic cod are most commonly found in temperature <2.5 °C (Wyllie-Echeverria and Wooster 1998; Rajasakaren 2013; Astthorsson 2016), though in laboratory studies, they achieve their maximum growth at 7 °C (Laurel et al. 2016). Early life stages (eggs and larvae) of Arctic cod may be more vulnerable to warmer temperatures. Egg hatch rates decline at temperatures exceeding 3 °C (Laurel et al. in press) and the upper thermal limits of heart function for larval cod are 3 °C cooler than for adults (Drost et al. 2016).

Compared with the rest of the globe, the Arctic is warming roughly twice as fast with sea temperatures expected to rise an additional 1.5° C by 2100 under moderate carbon emission scenarios (Collins 2013). Warming has resulted in a reduction of sea ice extent and thickness (age). From 1979-2018 there has been a reduction in September ice extent by 12.8% per decade (NSIDC 2018) and multi-year ice Arctic-wide (Perovich 2011). Increased open-water seasons will prolong the growing season for primary production (Brown and Arrigo 2012) due to an earlier ice retreat and earlier blooms (Kahru et al. 2010) with potential implications for organisms higher up the food chain. In addition, with longer ice-free seasons, there is an increased interest in shipping, oil exploration and expansion and/or development of commercial fisheries in the Arctic (currently prohibited in US Arctic waters – NPFMC 2009).

Currently, little is known about the life history of Arctic cod in the Pacific Arctic. Basic information on their biology (life history and vital rates) and a better understanding of their dynamics, population structure and distribution is needed for proper management. Current research and sampling in the region has been both facilitated by, and made more urgent, by the observed rapid changes in climate. In the first two chapters of this dissertation, I assess the trophic roles of Arctic cod and other common fish species, and the distribution and population dynamics of Arctic cod in the eastern Chukchi Sea. For this, I use samples and data collected during the Arctic Ecosystem integrated survey (Arctic Eis) in the summers of 2012 and 2013. Even though there have been several fisheries surveys within the Chukchi Sea (e.g., Norcross et

al. 2010), Arctic Eis was the first spatially comprehensive, quasi-synoptic fisheries oceanographic survey across water masses in the US portion of the Chukchi Sea.

The Chukchi Sea is characterized as a broad, shallow (average depth 80 m) continental shelf region that is seasonally ice covered. The ice retreat usually begins in May to early June with increased solar radiation and advection of warmer waters from the Bering Sea. Many biological processes are timed with the spring sea ice retreat, such as migration of fish, seabirds and marine mammals (e.g., Bluhm et al. 2007), advection of larval fish and plankton and the timing of the phytoplankton bloom (Kahru et al. 2011). The timing of fall ice formation also influences the transport of Bering Sea Water northward through Bering Strait into the Chukchi Sea (Weingartner et al. 2005). Waters from the Bering Sea are comprised of three water masses: the nutrient rich, relatively colder, and more saline Bering Sea (central) and Anadyr Waters (west), and the warmer, fresher and nutrient depleted Alaska Coastal Water in the east (Coachman et al. 1975). Mixing between the Anadyr Water and the Bering Shelf Water produces the combined Bering Chukchi Summer Water (BCSW) (Danielson et al. 2017). An additional water mass, the colder Resident Chukchi Water or Chukchi Winter Water (CWW) is found in the northern Chukchi Sea above 70–71°N and forms a semi-permanent front where it meets the Alaska Coastal Water (Weingartner 1997). These water masses are key in structuring zooplankton, pelagic and benthic fish communities in the northern Bering and southern Chukchi seas (Hopcroft et al. 2010, Norcross et al. 2010, Eisner et al. 2012).

In Chapter 1, I examined the trophic roles of different species in the fish community using stable isotope analysis, which provides an alternative and complimentary approach to diet analysis for assessing the trophic roles of organisms. The nitrogen isotope ratio, $\delta^{15}N$, is used to assess trophic level based on a consistent enrichment from prey to consumer (Minagawa and Wada 1984; Post 2002). In contrast, $\delta^{13}C$ is relatively conserved throughout the food web with minimal enrichment (0-1‰) and can be used to track diet sources and general feeding habitats (e.g., benthic versus pelagic (France 1995)). Unlike diet analysis, stable isotope analysis integrates only food items assimilated by consumers, accurately representing a transfer of energy from prey to consumer, and integrates diet over longer time-scales (Miller 2006). Trophic level ($\delta^{15}N$) often increases with body length (e.g., Marsh et al. 2012) and it is important to consider the trophic role of fish species throughout their life history.

I assessed the trophic roles (diet source and trophic level) of fishes collected during the 2012 and 2013 Arctic Eis survey using nitrogen and carbon stable isotopes. The main objectives were to: 1) describe ontogenetic trophic roles of common marine and anadromous fish species; 2) assess spatial variability in the stable isotope composition of the fish community by size class; 3) estimate community level measures to quantify isotopic niche space, trophic redundancy and trophic separation within each water mass; and to 4) assess the trophic role of a key species, Arctic cod, within the Chukchi Sea fish food web relative to water mass characteristics. I also created isoscapes (smooth spatial surface) of $\delta^{15}N$ and $\delta^{13}C$ for *Calanus* spp. to visualize variability at the base of the food chain and to correct the fish stable isotope values for this baseline variation, as both $\delta^{15}N$ and $\delta^{13}C$ of primary producers can vary across time and space (Goericke and Fry 1994; Vander Zanden and Rasmussen 1999). For objective 1, I hypothesized that individual species have unique trophic levels ($\delta^{15}N$) that change with body length and that diet source ($\delta^{13}C$) changes with body length. For objective 2, I hypothesized that stable isotope composition of fish communities varies spatially across the Chukchi Sea with the values reflecting source waters (baseline, pelagic versus benthic, trophic level). Examining how spatial gradients in trophic levels are linked their environment can provide insight into potential shifts in Arctic cod and other Arctic fishes with a changing climate

After researching Arctic cod's trophic role in Chukchi Sea food webs, I examined their distribution and population dynamics in the Chukchi Sea in Chapter 2. Currently, commercial fishery removals are prohibited in the US Arctic (NPFMC 2009), but questions remain if the US Chukchi Sea can support a commercial fishery. No commercial fisheries on Arctic cod have been reported in FAO statistical area 18 (Zeller et al. 2011), which includes the Chukchi Sea. However, in the Northeast Atlantic (captured by FAO statistical area 27), an Arctic cod fishery began in the 1950s, peaked at over 348,000 mt in 1971 (Gjøsæter 1995) and continues today at much reduced levels with 19,600 mt removed by Russia in the Barents Sea in 2011 (ICES 2012). Small amounts of Arctic cod are also caught in subsistence fisheries in the Beaufort and Chukchi seas (Magdanz et al. 2010). Arctic cod have slow growth rates, early maturation, and a short life-span, usually less than 5 years (Bradstreet et al. 1986). Past fisheries have found commercial uses for Arctic cod and have also suggested that the stock may recover quickly from overfishing (Monstad and Gjøsæter 1987). However, removals of Arctic cod could affect upper trophic levels because of the central role of Arctic cod in the Arctic food web. Prolonged open water

seasons coupled with warming waters and changing ranges of fish species may create conditions that could lead to an interest in commercial fishery development or expansion in the Alaskan Arctic (NPFMC 2009).

Using data from Arctic Eis surveys in the Chukchi Sea during 2012 and 2013 and available estimates of biological parameters (e.g., fecundity, growth, survival), I examined drivers of distribution and abundance, and assessed the current status and dynamics of Arctic cod. My primary objectives were to: 1) improve our understanding of the distribution and abundance of Arctic cod and the biological and environmental factors driving their variation in the eastern Chukchi Sea; and 2) assess their current status and their potential for supporting a fishery. To address objective 1, I quantified the distribution and abundance of Arctic cod relative to environmental (temperature and salinity) and biological (food availability, potential predators, competitors) factors to identify what may determine spatial patterns in CPUE (catch per unit effort). For objective 2, I compiled and updated available life history information for Arctic cod in the Chukchi Sea and updated the preliminary stock assessment of Arctic cod in the Arctic Fisheries Management Plan (NPFMC 2009) using recent survey data for the Chukchi Sea (2012 and 2013) and updated life history information. Based on updated abundance estimates, I estimated total egg production to determine if the estimated adult population from the 2012 bottom trawl survey could likely produce the high abundance of age-0 Arctic cod estimated from a 2013 acoustic survey (De Robertis et al. 2017).

Finally, in chapter 3, I examined environmental and biological influences on Arctic cod distribution at the southern edges of their distribution in the Atlantic and Pacific Oceans. Arctic cod have a circumpolar distribution that extends into sub-Arctic seas in both the Atlantic and Pacific Oceans. The entry points into the Arctic Ocean can be characterized as either inflow or outflow shelves (Carmack and Wassmann 2006): the Bering Strait / Chukchi Sea in the Western Hemisphere (inflow shelf), the Canadian Archipelago and Davis Strait between Greenland and Canada (predominately outflow), the East Greenland shelf (outflow) and the Barents Sea (predominately inflow). In chapter 3, I focus on the distribution of Artic cod in the Bering Sea south of the Bering Strait and on the Labrador Newfoundland Shelf Region (LNR) south of Davis Strait. In the Bering Sea there is a persistent deep cold pool (< 2°C) over the middle of the shelf driven by winter sea-ice and protected from summer mixing by the thermocline that may act as a thermal barrier to subarctic fish expanding northward (Sigler et al. 2011). From the

1980s through the mid-2000s, the cold pool retreated approximately 230 km northward (Mueter and Litzow 2008), from 2007 through 2013 it advanced (Kotwicki and Lauth 2013) and has since retreated (Siddon and Zador 2017). In the summer of 2018, it was nearly nonexistent (R. Lauth, NOAA-AFSC, Seattle, pers. comm.). In the LNR, there is a cold intermediate layer (<0 °C) that impinges on the bottom near the coast and extends out to 200-300 km (Petrie 1988) where it occurs over saltier and warmer (3 – 4 °C) Labrador Slope water (Colbourne et al. 2017). The area of cold intermediate layer was anomalously larger from the mid-1980s to the 1990s, smaller from 1995 to 2014 and intermediate in recent year over a time series including years from 1950 – 2017 (Colbourne et al. 2017).

In chapter 3, the goal of the study was to explore what limits the southern distribution of Arctic cod in the Pacific and Atlantic sectors by examining time series of survey and oceanographic data across regions. The main objectives were to 1) quantify the interannual variability of distribution of Arctic cod in the eastern Bering Sea and Newfoundland and Labrador shelves, 2) examine the influence of temperature on variability of the distributions and, 3) examine the influences of potential competitors, predators and temperature on Arctic cod distribution using time series of survey data from the eastern Bering Sea and from the Labrador Sea. Understanding how environmental variability, especially in temperature, and the abundance of potential predators and competitors affect Arctic cod distributions will aid in predicting distributions of Arctic cod under future climate scenarios.

Chapter 1 Ontogenetic, spatial and temporal variation in trophic level and diet of Chukchi Sea fishes[1]

1.1 Abstract

Climate warming and increasing development are expected to alter the ecosystem of the Chukchi Sea, including its fish communities. As a component of the Arctic Ecosystem Integrated Survey, we assessed the ontogenetic, spatial and temporal variability of the trophic level and diet of key fish species in the Chukchi Sea using N and C stable isotopes. During August and September of 2012 and 2013, 16 common fish species and two primary, invertebrate consumers were collected from surface, midwater and bottom trawls within the eastern Chukchi Sea. Linear mixed-effects models were used to detect possible variation in the relationship between body length and either $\delta^{13}C$ or $\delta^{15}N$ values among water masses and years for 13 fish species with an emphasis on Arctic cod (*Boreogadus saida*). We also examined the fish community isotopic niche space, trophic redundancy, and trophic separation within each water mass as measures of resiliency of the fish food web. Ontogenetic shifts in trophic level and diet were observed for most species and these changes tended to vary by water mass. As they increased in length, most fish species relied more on benthic prey with the exception of three forage fish species (walleye pollock, *Gadus chalcogrammus*, capelin, *Mallotus villosus*, and Pacific sandlance, *Ammodytes hexapterus*). Species that exhibited interannual differences in diet and trophic level were feeding at lower trophic levels and consumed a more pelagic diet in 2012 when zooplankton densities were higher. Fish communities occupied different isotopic niche spaces depending on water mass association. In more northerly Arctic waters, the fish community occupied the smallest isotopic niche space and relied heavily on a limited range of intermediate $\delta^{13}C$ prey, whereas in warmer, nutrient-rich Bering-Chukchi summer water, pelagic prey was important. In the warmest, Pacific-derived coastal water, fish consumed both benthic and pelagic prey. Examining how spatial gradients in trophic position are linked to environmental drivers can provide insight into potential fish community shifts with a changing climate.

[1] Marsh, J.M., Mueter, F.J., Iken, K. and Danielson, S., 2017. Ontogenetic, spatial and temporal variation in trophic level and diet of Chukchi Sea fishes. *Deep Sea Research Part II: Topical Studies in Oceanography*, *135*, 78-94.

1.2 Introduction

Marine ecosystems can be defined and compared by their trophic structure (Lindeman 1942), which may be altered through climate-driven changes in productivity (bottom-up processes), or through predator removals by fishing and alterations in predator range (top-down processes). For example, following a climate shift to a warm regime in the 1970s in the Gulf of Alaska, a community-wide trophic restructuring occurred. The system switched from an ecosystem dominated by benthic crustaceans and forage fish to one dominated by higher trophic level predatory groundfish (Anderson and Piatt, 1999), leading to an increase in trophic level (TL) of the fishery catches from the 1970s through the early 1990s (Urban and Vining, 2008). Conversely, in the North Atlantic, fishing pressure on predatory groundfish, combined with oceanographic changes, resulted in a switch from an ecosystem dominated by demersal fishes to one dominated by small pelagic fishes, benthic crustaceans and bivalves (Frank, 2005). Most likely, the effects of climate and fishing pressure worked synergistically to restructure that ecosystem (Kirby et al., 2009). Therefore, while it can be difficult to tease apart the effects of climate change and fisheries removals on ecosystem structure, the combined effects can be dramatic.

Commercial fishery removals are currently prohibited in the US Arctic, i.e., the eastern Chukchi and western Beaufort seas (NPFMC, 2009), a region impacted by extreme seasonality and pronounced climate change (ACIA, 2004). By 2100, air and sea temperatures in the Arctic are expected to rise an additional 5° C and 1.5° C, respectively, under moderate carbon emission scenarios (Collins 2013). Moreover, the annual average Arctic sea ice extent has shrunk by 3.5 – 4.1% per decade, with larger decreases of 9.4% per decade (1979-2012) occurring in the summer (Collins 2013). It has been suggested that the central Arctic Ocean will be seasonally ice-free as early as 2040 (Holland, et al., 2006; Wang and Overland, 2012). With warming and a longer open-water season there is an increased interest in shipping, oil exploration and development/expansion of commercial fisheries. Until the fisheries ban is lifted and/or the Arctic Ocean is seasonally ice-free, the Arctic Ocean offers an opportunity to study effects of climate change with limited confounding from anthropogenic activities.

Future effects of continued climate warming and potential anthropogenic disturbances might have large impacts on the Chukchi Sea ecosystem. Warming waters and reduced extent of the Bering Sea cold-pool, a persistent pool of cold (<2°C) bottom water formed during sea ice

brine rejection that acts as a thermal barrier to the expansion of subarctic fishes northward (Mueter and Litzow, 2008), may facilitate earlier seasonal migrations (Moss et al., 2009) or the establishment of some subarctic fishes in the Arctic (Hollowed et al., 2013). These changes could alter Chukchi food web structure through changes in predation and competition for food resources. Also, earlier ice retreat and a prolonged open-water season could lead to earlier phytoplankton blooms and extended growing seasons (Kahru et al., 2011). Observed and future changes in phytoplankton bloom timing and composition (Li et al., 2009), along with changes in zooplankton composition, increases in abundance (Ershova et al., 2015) and grazing pressure (Lane et al., 2008), could possibly weaken the currently strong pelagic-benthic coupling. Currently, cold temperatures in the spring and summer limit zooplankton growth and reproduction; therefore, much of the primary production (ice algae and phytoplankton) is not heavily grazed and settles from the water column to support high benthic biomass (Coyle and Pinchuk, 2002; Questel et al., 2013). These effects will most likely vary spatially, as water mass structure has a strong influence on the community composition and food web structure of the biota (Eisner et al., 2012; Iken et al. 2010). Fishes provide important links between lower and upper trophic levels, as well as between benthic and pelagic communities. Therefore, changes in trophic structure experienced by the fish community may alter the efficiency of the food web with important consequences for upper trophic level species, including seabirds and mammals important to subsistence in coastal communities.

The pelagic and demersal fish biomass in the Chukchi Sea is generally low compared with invertebrate biomass (Stevenson and Lauth, 2012). In previous surveys, 59 demersal fish species in 17 families have been identified in the Chukchi Sea (Barber et al., 1997; Norcross et al., 2010, 2013). However, only 4 families and 10 species comprise the majority of the demersal fish community (~90%): Gadidae (Arctic cod *Boreogadus saida,* saffron cod *Eleginus gracilis*), Cottidae (Hamecon *Artediellus scaber*, Arctic staghorn sculpin *Gymnocanthus tricuspis*, shorthorn sculpin *Myoxocephalus scorpius*), Pleuronectidae (Bering flounder *Hippoglossoides robustus,* yellowfin sole *Limanda aspera,* Alaska plaice *Pleuronectes quadrituberculatus*), and Zoarcidae (polar eelpout *Lycodes polaris*) (Barber et al., 1997; Norcross et al., 2013). Even fewer species have been observed in the pelagic fish community with the dominant species being Pacific herring (*Clupea pallasii*), juvenile chum salmon (*Oncorhynchus keta*), juvenile Arctic cod (*Boreogadus saida*), capelin (*Mallotus villosus*) and Pacific sandlance (*Ammodytes*

hexapterus) (Eisner et al., 2012). These species tend to be segregated into three groups: cold-adapted polar species, coastal species, and Pacific species (Barber et al., 1997; Norcross et al., 2010). Moreover, species richness declines from warmer sub-arctic waters to cooler Arctic waters in the northern Chukchi Sea (Mueter et al., 2013), as well as from nearshore to offshore (Barber et al., 1997; Piatt and Springer, 2003). In previous surveys of the Chukchi Sea, Arctic cod have consistently been one of the most dominant species, in terms of both biomass and abundance, in both pelagic and demersal trawls (Barber et al., 1997; Eisner et al., 2013; Norcross et al., 2010, 2013). This species plays a crucial role in the ecosystem as important prey for many migrating seabirds (Matley et al., 2012) and marine mammals (Bluhm et al., 2008; Crawford et al., 2015; Loseto et al., 2009). Arctic cod are considered a key species linking upper and lower trophic levels in a relatively simple food web (Whitehouse et al., 2014).

To evaluate potential future changes in the fish community it is necessary to understand the diets of different species. Stable isotope analyses provide an alternative and complementary approach to the more traditional stomach content diet analyses. Two stable isotopes, ^{15}N and ^{13}C, are commonly used to characterize trophic status and dynamics. The ratio of heavy to light nitrogen relative to a standard ($\delta^{15}N$) is used to assess trophic level based on a distinct stepwise enrichment from prey to consumer (Minagawa and Wada, 1984; Post, 2002). In contrast, $\delta^{13}C$ is conserved throughout the food web with minimal enrichment between trophic levels (0-1‰) and can be used to track diet sources and general feeding habitats; e.g., phytoplankton tends to be more depleted in ^{13}C than benthic primary producers (France, 1995). Unlike stomach content analysis, stable isotope analysis integrates only food items assimilated by consumers, accurately representing a transfer of organic matter between trophic levels, and integrates diet over time-scales ranging from weeks to months, depending on the tissue analyzed (Miller, 2006). Previous studies using C and N stable isotopes to examine the diets and trophic levels of fauna in the Chukchi Sea have primarily examined benthic organisms, including fishes, but have been limited by small samples sizes and/or spatial coverage (Feder et al., 2011; Iken et al., 2010; McTigue and Dunton, 2014). Studies of a few replicates (usually 1-9 specimens of each fish species collected per water mass) have found differences in fish trophic levels between water masses. Because trophic level (based on $\delta^{15}N$) often increases with body length (e.g., Jennings et al., 2002; Marsh et al., 2012) it is important to consider the trophic position of fish species throughout their life history. For example, the stable isotope signatures of different size classes

of five common fish species within a limited region of the northeastern Chukchi Sea typically had higher $\delta^{15}N$ values in larger size classes of Bering flounder (*H. robustus*), Arctic cod, polar eelpout (*L. polaris*), Arctic staghorn sculpin (*G. tricuspis*) and stout eelblenny (*Anisarchus medius*) (Edenfield et al., 2011). Here we build on the previous work by conducting a spatially comprehensive stable isotope study.

As a component of the Arctic Ecosystem Integrated Survey, this project presents a unique opportunity to assess the ontogenetic, spatial and temporal variability of the trophic level and diets of key fish species in the eastern Chukchi Sea using C and N stable isotope data, complementing ongoing stomach content studies in the region. In addition, we use community level measures to quantify isotopic niche space, trophic redundancy and trophic separation within each water mass. Our specific objectives are to: (1) create isoscapes of C and N stable isotope ratios based on the primary consumer *Calanus* spp. to quantify and visualize spatial isotopic gradient at the base of the pelagic food web; (2) describe the ontogenetic diets and trophic level of common marine and anadromous fish species in the eastern Chukchi Sea; (3) assess spatial variability in the stable isotopic composition of the fish community by size class; and (4) assess the trophic role of a key species, Arctic cod, within the Chukchi Sea fish food web relative to water mass characteristics. We hypothesize that individual species have unique trophic levels (based on $\delta^{15}N$) that change with body length and that diet source (based on $\delta^{13}C$) changes with body length. We further hypothesize that the stable isotope composition of fishes varies spatially across the Chukchi Sea, reflecting different source waters and communities.

1.3 Methods

1.3.1. Study Region

The Chukchi Sea is a broad, shallow (typical depth 50 m) continental shelf region marked by extreme seasonality: dark ice-covered winters versus long days and open water in the summer. Many biological processes are timed to coincide with the spring sea ice retreat, such as migration of fish, seabirds and marine mammals (e.g. Bluhm et al., 2007; Mecklenburg et al., 2011), advection of larval fish and plankton and the timing of the phytoplankton bloom (Kahru et al., 2011). Typically, the ice retreat begins in May to early June with increased solar radiation and advection of warmer waters from the Bering Sea. Three water masses flow northward

through the Bering Strait: the nutrient-rich, relatively colder, and more saline Anadyr Water (west), the warmer, fresher and nutrient-depleted Alaska Coastal Water (ACW) in the east, and a shelf mixture of these two water masses with intermediate nutrients levels, temperatures and salinity known as Bering Shelf Water (central) (Coachman et al., 1975). Mixing between the Anadyr Water and the Bering Shelf Water produces the combined Bering Chukchi Summer Water (BCSW) (Danielson et al., 2017). There is typically a strong density front separating the Alaska Coastal Current and the Bering Shelf Water (Grebmeier et al., 1988). An additional water mass resulting from brine rejection during ice formation in winter is the colder and more saline Chukchi Winter Water (CWW; Danielson et al., 2017). In late summer, CWW is commonly found in the lower portion of the water column on the northern Chukchi shelf, often but not always topographically confined to the Hanna Shoal region. The relatively fresh and cold Melt Water (MW) derived from pack ice melt can occupy surface waters in the open water season following the receding ice edge. Finally, the dense and saline (>33.5) Atlantic Water (ATL) is observed in the near-bottom waters (> 200 m depth) at the mouth of Barrow Canyon on the continental slope (Danielson et al., 2017). The distribution and spatial extent of these water masses within the eastern Chukchi Sea is likely to vary in response to both local atmospheric forcing and variability in oceanic advection (Weingartner et al., 2005).

These water masses are key in structuring zooplankton, pelagic fish and demersal fish communities in the northern Bering and southern Chukchi Seas (Eisner et al., 2012; Hopcroft et al., 2010; Norcross et al., 2010; Sigler et al., 2017). Specifically, the fish communities are split into a coastal group in the ACW, a "Pacific-dominated" group in the BCSW, and true Arctic fishes in the CWW (Norcross et al., 2010). The BCSW is characterized by high primary and secondary productivity due to high nutrient availability, a large influx of zooplankton advected from the south, and high benthic biomass (Grebmeier et al., 1988; Walsh et al., 1989). The CWW also tends to have high nutrient concentrations, while the ACW has the lowest concentrations of nutrients and marine carbon during the summer (Walsh et al., 1989).
There is strong connectivity between the water masses and marine communities in the northern Bering and Chukchi seas because of the northward flow through the Bering Strait. Aside from nutrients, heat and freshwater, the Pacific water brings with it biota into the Chukchi Sea. The net northward flow (~0.8 Sv annually) of Pacific Ocean water through the narrow (~80 km) and shallow (<50 m) Bering Strait to the Arctic Ocean is driven by a sea surface height difference

between the fresher Pacific Ocean and the more saline Atlantic Ocean (Aagaard et al., 2006). Transport through the Bering Strait varies on interannual, seasonal and shorter time scales related to the position of the Aleutian Low and local winds (Danielson et al., 2014). The flow is greatest in the summer months and least in the winter when the Bering Strait and Chukchi Sea are covered with ice and opposing winds are strong (Woodgate, 2005a). There are occasional wind-driven reversals in flow between November and March (Woodgate et al., 2006). About 20% of the northward flow is comprised of ACW, which is present from May through December (Woodgate, 2005b). Although flow through the Bering Strait is clearly important to the fish community, the role of advection versus local production in structuring and maintaining the fish communities in the Chukchi Sea is poorly understood.

1.3.2. Sample Collection

All samples for this study were collected during two comprehensive fisheries oceanographic surveys in August/September 2012 and 2013 within the eastern Chukchi Sea (Figure 1.1). Surveys included oceanography, acoustics, zooplankton, and surface and midwater trawls conducted aboard the F/V Bristol Explorer. During the standardized grid survey, stations were sampled every ~55 km (61 stations in 2012 and 40 in 2013) with additional stations for oceanographic and plankton collections every ~ 28 km along E-W transects (45 stations in 2012 and 62 in 2013). Pelagic fish samples were collected with a 400/601 Cantrawl from the upper 25-30 m of the water column at each main station and opportunistically at locations with a strong acoustic signal by midwater trawls using the same 400/601 Cantrawl as well as a modified Marinovich trawl (2013 only). The 400/601 Cantrawl net was 198 m long with a 122 m headrope and had mesh tapering from 162 to 1.2 cm at the cod-end liner, while the modified Marinovich trawl was ~31 m long with meshes tapering from 6.4 to 0.3 cm at the cod-end liner. Zooplankton samples were collected using 60-cm (505 μm mesh) and 20-cm (153 μm mesh) paired bongos obliquely towed from near bottom to the surface. At each station a conductivity, temperature and depth meter (CTD) collected data throughout the water column (SBE 9-11 plus or FastCat CTD, Sea-Bird Electronics, Inc, Bellevue, WA). In 2012 only, demersal fishes and benthic invertebrates were collected concurrently at 71 main stations aboard the F/V Alaskan Knight, using an 83-112 Eastern bottom trawl (EBT; 25.3 m head rope, a 34.1 m footrope and 32 mm mesh cod-end liner) and, at selected stations, a plumb staff beam trawl (4.1 m headrope, 5.1 m

footrope and a 4 mm mesh cod-end liner) (Fig 1). An RDI Citadel CTD was attached to the headrope of the EBT.

Diets by size, as inferred from stable isotopes, were assessed for the most common fish species in the Chukchi Sea (Norcross et al., 2010; Eisner et al., 2012), as well as less common species including capelin and walleye pollock (Table 1). We also collected pelagic and benthic primary consumers as baseline organisms to define the natural spatial and temporal isotope variation at the base of the food web (Table 1). When available, 30 specimens per species were collected from each water mass (Alaska Coastal Water, Bering Chukchi Summer Water, Melt Water (surface) and Chukchi Winter Water (bottom)), based on post-hoc analyses of CTD data, for stable isotope analysis. A sample size of 30 was selected in order to detect a 0.25 change in trophic level over 80% of the maximum length of a given species with 80% power (Galván et al., 2010). Fishes were identified to species, total length measured to the nearest mm, labeled with haul information, and individually frozen for further processing. Where available, 30 *Calanus* spp. were collected from the 150 μm mesh bongo and frozen to a glass slide at each surface trawl station to represent pelagic baseline consumers. Up to 3 bivalves (*Serripes groenlandicus*) were retained as a benthic baseline consumer at each station on the bottom trawl survey, as this species presents a long-lived integrator of carbon and nitrogen available to benthic organisms. Due to limited spatial coverage of *S. groenlandicus*, only *Calanus* spp. were used to convert study organism $\delta^{15}N$ values to trophic level and to correct for both $\delta^{15}N$ and $\delta^{13}C$ baseline variation (see analysis section). In addition to being a prey item for all of the surface trawl caught and some of the bottom trawl caught fish species, *Calanus* spp. also was chosen as a baseline organism because samples were available from most of the sampling sites, allowing us to quantify spatial differences in the baseline values of $\delta^{15}N$. Moreover, *Calanus* spp. were collected throughout the water column and has some degree of spatial overlap with all of the targeted fish species.

1.3.3. Sample processing

In the lab, samples were prepared for stable isotope analysis (SIA). From minimally thawed fishes, approximately 0.5 g of dorso-lateral muscle were excised with skin and bones carefully removed. For smaller (age-0) fishes, the head, guts and tail were removed and the remainder was retained for SIA. Also, muscle tissue from *S. groenlandicus* samples, and whole-

body *Calanus* spp. (8-12 per sample x 3 samples/station) were analyzed for $\delta^{15}N$ and $\delta^{13}C$. Samples were placed into 20 ml glass scintillation vials, freeze-dried and pulverized with a glass rod. For each sample, 0.2-0.5 mg of muscle tissue, or homogenized copepods were weighed out and enclosed in a tin capsule for SIA. Samples were analyzed at the Alaska Stable Isotope Facility (UAF) for nitrogen and carbon stable isotopes using a Costech ECS4010 elemental analyzer interfaced through a CONFLO III to a Finnigan Delta^{plus}XP isotope ratio mass spectrometer (IRMS). Results are presented in delta (δ) notation in per mil (‰) calculated using the following formula:

$$\delta X = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1{,}000$$

where X is ^{15}N or ^{13}C and R is the ratio of heavy to light isotope ($^{15}N/^{14}N$ or $^{13}C/^{12}C$) for a given element. The standards are Vienna Pee Dee Belemnite for $\delta^{13}C$ and atmospheric air for $\delta^{15}N$. The isotope ratio mass spectrometer precision values were 0.17‰ for $\delta^{13}C$ and 0.32‰ for $\delta^{15}N$ based on the standard deviation of replicates of peptone, which were run on every 10th sample (n = 290). About 15 samples with unlikely values, which may have resulted from sample contamination or mechanical error, were re-analyzed for C and N stable isotopes. The newer values replaced the original values and were used in analyses.

1.3.4 Data analysis

Lipids tend to be relatively more depleted in ^{13}C than proteins (DeNiro and Epstein, 1977). To account for varying lipid contents in our samples (fishes and bivalves), we used an arithmetic lipid normalization equation generalized for aquatic organisms (Post, Layman et al. 2007):

$$\delta^{13}C' = \delta^{13}C - 3.32 + 0.99 \cdot C{:}N$$

where $\delta^{13}C'$ is the lipid normalized value, $\delta^{13}C$ is the value from the bulk tissue, and C:N is the carbon to nitrogen ratio for each sample. *Calanus* copepods tend to have a much higher lipid content than fish muscle, thus a similar arithmetic lipid normalization equation specifically for copepods was applied to *Calanus* samples (El-Sabaawi et al., 2008)

$$\delta^{13}C' = \delta^{13}C - 1.85 + 0.38 \cdot C{:}N$$

1.3.4.1 Isoscapes

We constructed smooth spatial surfaces, or isoscapes, of $\delta^{15}N$ and $\delta^{13}C$ for baseline organisms to visualize variability at the base of the food chain and to correct the fish stable isotope values for this baseline variation. Both $\delta^{15}N$ and $\delta^{13}C$ values of primary producers can vary in space and time (Holst Hansen et al., 2012; Schell et al., 1998; Vander Zanden and Rasmussen, 1999). In order to compare fish stable isotope values across the eastern Chukchi Sea, it is important to correct for these natural spatial variations because, for example, elevated $\delta^{15}N$ values could result either from fish feeding at a higher trophic level or from a higher baseline $\delta^{15}N$ value. Therefore, we corrected for baseline variation by subtracting estimated $\delta^{15}N$ and $\delta^{13}C$' anomalies for the primary consumer *Calanus* spp. from the corresponding values for each fish species at a given location.

Stable isotope anomalies for the baseline organism throughout the study region were estimated by fitting a geospatial model to observed anomalies in $\delta^{15}N$ or $\delta^{13}C$' for *Calanus* spp. The observed anomalies were computed by subtracting the mean values for $\delta^{15}N$ or $\delta^{13}C$' across all stations from the station-specific means. Models were fit via universal or ordinary kriging, a geostatistical interpolation technique that exploits spatial autocorrelation (nearby values will tend to be more similar) in the observed anomalies, after removing any trends. Specifically, we first removed linear spatial trends from $\delta^{13}C$', but not from $\delta^{15}N$ because no linear trends in $\delta^{15}N$ were apparent. We then used weighted least squares to fit exponential semi-variogram models to the residuals for $\delta^{15}N$ and $\delta^{13}C$', respectively. Models were fit separately for 2012 and 2013 to account for interannual differences in baselines. For all semi-variogram models, the nugget was set to 0.2 to account for moderate within station variability. Predicted values were then estimated over a grid covering the entire study area to construct *Calanus* spp. $\delta^{15}N$ and $\delta^{13}C$' isoscapes for visual assessment. Raw $\delta^{15}N$ and lipid normalized $\delta^{13}C$' stable isotope values for each fish sample were adjusted ($\delta^{15}N_{adj}$ and $\delta^{13}C_{adj}$) by subtracting the kriged $\delta^{15}N$ and $\delta^{13}C$ baseline anomalies from the corresponding values for fish at each sampling location. Geospatial models were fit using the R package geoR (Diggle and Ribeiro, 2007; Ribeiro and Diggle, 2001). Two unrealistic 2013 *Calanus* spp. replicate samples were removed prior to analysis. The $\delta^{15}N$ values of these samples were >3‰ different than the other two replicates at the same station and were assumed to be due to an error.

In addition to the adjusted N isotope ratio ($\delta^{15}N_{adj}$), we computed the corresponding trophic levels of each sample to provide values in a more intuitive framework. Trophic levels relative to the baseline were estimated from $\delta^{15}N_{adj}$ values for each fish sample (Post, 2002) and the trophic levels of individual species and communities were compared across water masses. We assumed that $\delta^{15}N$ has a constant enrichment of 3.4‰ from diet to consumer (Minagawa and Wada 1984; Post 2002). In order to estimate the TL based on $\delta^{15}N$ data, we used the following equation:

$$TL_i = \left(\frac{\left(\delta^{15}N_{adj,i} - \delta^{15}N_{ref}\right)}{3.4}\right) + TL_{ref}$$

where TL_i is the trophic level of each individual i, $\delta^{15}N_{adj,i}$ is the adjusted nitrogen stable isotope ratio for each individual i, $\delta^{15}N_{ref}$ is the estimated mean $\delta^{15}N$ value for the baseline organism *Calanus* spp. in either 2012 or 2013, and TL_{ref} is the TL of 2.0 assigned to the generally herbivorous *Calanus* spp. (Hobson et al., 2002; Wang et al., 2015).

Finally, we ran linear regressions of the unadjusted $\delta^{15}N$ and $\delta^{13}C$' values for each fish species on the modeled baseline values to determine how much variation in the fish stable isotope values were explained by the baseline variation.

1.3.4.2 Water mass classification

Water mass structure in the Chukchi Sea is known to influence community composition (Eisner et al., 2013) and food web structure (Iken et al., 2010); therefore, we defined water masses for use in further analyses of trophic structure. Water masses were defined based on temperature-salinity (T-S) characteristics that could reflect different times of formation, spatial distributions, or ecological importance. Near-bottom temperatures and salinities represent averages over the bottom 5 m of the CTD profile, and surface layer values are averages from the upper 10 m of the water column. T-S plots were visually assessed for modes such that the resulting water masses had similar characteristics to previously defined water masses in the Chukchi Sea (Alaska Coastal Water = ACW, Bering Chukchi Summer Water = BCSW, Melt Water = MW, Chukchi Winter Water = CWW) (Coachman et al., 1975; Danielson et al., 2017; Eisner et al., 2013; Gong and Pickart, 2015; Weingartner, 1997). Often the mixed layer depth (transition zone between the lower density surface water and higher density bottom layer) was less than 10 m, while the vertical spread of the surface trawl net averaged 17 m and the actual tow depth extended roughly 5 m below that depth. We paired the observed surface and bottom

water mass types at each sampling location into distinct water mass structures, including ACW, ACW/BCSW, BCSW, MW/BCSW, BCSW/CWW and MW/CWW, where MW/CWW, for example, denotes surface Melt Water overlaying Chukchi Winter Water and ACW denotes the presence of Alaska Coastal Water throughout the water column.

1.3.4.3 Ontogenetic shifts

To address objective 2, we modeled $\delta^{13}C'_{adj}$ or $\delta^{15}N_{adj}$ for each species as a function of body length, water mass, and year. We pooled all fishes from the 2012 surface trawl survey and bottom trawl survey to assess ontogenetic shifts in trophic roles between water masses. To examine interannual variability in trophic roles, only fish collected during surface trawl surveys in 2012 and 2013 were used. Prior to model fitting, $\delta^{13}C'_{adj}$ and $\delta^{15}N_{adj}$ values for fish collected in 2013 were further adjusted by the differences in mean $\delta^{13}C'$ and $\delta^{15}N$ values for *Calanus* spp. between years to compare isotopic enrichment relative to the respective baselines. Linear mixed-effects models were used to quantify how $\delta^{13}C'_{adj}$ or $\delta^{15}N_{adj}$ vary with body length and how this relationship varies among water masses and between years (the latter for surface trawl-caught species only). The isotope ratios ($\delta^{13}C'_{adj}$ or $\delta^{15}N_{adj}$) were modeled as a function of length for each species because ontogenetic shifts in feeding often result in changes of trophic level and foraging habitat. These relationships are often not linear and we observed curvature in some plots of isotope values against raw length that suggested a log-linear relationship, thus three alternative models were fit allowing for either a linear, log-linear or quadratic relationship between length and $\delta^{13}C'_{adj}$ or $\delta^{15}N_{adj}$. The effects of water mass and year were analyzed separately. The full quadratic model includes main effects for year (surface trawl samples only) and water mass, and separate slopes for length by year and/or water mass, as well as random effects by station:

$$Y_{tkji} = \alpha_{tk} + \beta_{1tk}(Length) + \beta_{2tk}(Length)^2 + a_j + b_j(Length) + \varepsilon_{tkji}$$

where α_{tk} is the intercept for year t and water mass k, β_{1tk} is the coefficient (slope) for length in year t and water mass k, β_{2tk} is a quadratic coefficient for length^2 in year t and water mass k, a_j and b_j are random effects that capture station-specific deviations (station j) from the mean intercept and slope for a given year and water mass and ε_{tkji} is a residual for the i^{th} sample. The random effects a_j and b_j are assumed to follow a bivariate normal distribution:

$$\begin{bmatrix} a_j \\ b_j \end{bmatrix} \sim N(0, \boldsymbol{\Psi_1})$$

where $\boldsymbol{\Psi_1}$ is a 2x2 variance-covariance matrix with variances σ_a^2 and σ_b^2 and covariance $\sigma_{a,b}$. The residuals, ε_{tkji} are assumed to follow a normal distribution with mean 0 and variance σ_ε^2 and are assumed to be independent of the random effects. To find the optimal structure of the random component of the model, we compared the fit of the full model with random slopes (b_j) and intercepts (a_j) to a model with random intercepts only and to a model with no random component besides the residuals. All candidate models were compared using Akaike's information criterion (AIC) to identify the random structure that is most consistent with the data (Akaike, 1974). After we selected the random effects structure, the fit of the full model was compared to all possible reduced models and alternative models with ln(length), for which the full model is shown below:

$$Y_{tkji} = \alpha_{tk} + \beta_{tk}(\ln(Length)) + a_j + b_j(\ln(Length)) + \varepsilon_{tkji}$$

We used AIC to identify the model that was most consistent with the data. When the difference in AIC values was < 2, the more parsimonious model (fewer parameters) was selected. Maximum likelihood estimation was used for model comparisons, while restricted maximum likelihood estimation (Harville, 1977) was used for final parameter estimates. All linear mixed-effects models were fit using the 'nlme' package version 3.1-119 (Pinheiro et al., 2015) in the statistical program R (R Core Team, 2014). Goodness of fit was assessed using marginal R^2 (proportion of variance explained by the fixed factor(s) alone) and conditional R^2 (proportion of variance explained by both the fixed and random factors in combination) for linear mixed effects models (Nakagawa and Schielzeth, 2012) and the R^2 for linear models. Results from the best-fit models whose conditional R^2 exceeded 0.2 were visualized as follows. The estimated fixed effects showing the relationship between length and $\delta^{13}C'_{adj}$ or $\delta^{15}N_{adj}$ were plotted for each species and for each of the most common water masses (ACW, BCSW and MW/CWW) sampled in 2012.

1.3.4.4 Arctic cod

To visualize differences in the isotopic niche space of Arctic cod between years, water masses and size class, standard ellipse areas (multivariate mean ± SD) were estimated and plotted using the R package 'siar'. Standard ellipse areas contain 40% of the data points (area encompassing $\delta^{13}C'_{adj}$ and $\delta^{15}N_{adj}$ values on a $\delta^{13}C$-$\delta^{15}N$ bi-plot - the larger the area, the more varied the diet).

We examined elemental carbon to nitrogen ratios (C:N) as an index of lipid content and body condition. Higher lipid tissues have higher C:N (McConnaughey and McRoy, 1979) and may indicate a higher relative body condition. Specifically, we modeled C:N for Arctic cod as a function of body length, water mass, and year using the equations in section 2.4.3. To examine potential differences between water masses, we included all Arctic cod sampled in 2012 in our analysis. We also tested for potential interannual differences between the surface trawl caught Arctic cod in 2012 and 2013. Only fish that were sampled in water masses that occurred in both years were included in this analysis. Three outlying C:N values with standardized residuals that exceeded 5 were removed from the analysis because they potentially included non-muscle tissue.

1.3.4.5 Community isotopic space

To compare fish community trophic structure between water masses we estimated the community isotopic niche space and associated metrics in each water mass (Layman et al., 2007). The isotopic niche space is a measure of diet breadth of the fish community, here defined as the area contained within the smallest convex hull polygon surrounding the mean $\delta^{15}N_{adj}$ and $\delta^{13}C'_{adj}$ for each species-size class combination within each water mass. We calculated mean nearest neighbor distance as a measure of trophic redundancy (smaller distances implying higher redundancy), mean distance to centroid as a measure of trophic separation, $\delta^{15}N_{adj}$ range as a measure of food chain length and $\delta^{13}C'_{adj}$ range as a measure of diversity of basal food sources (Layman et al., 2007). These metrics were calculated using the R package 'siar' (Jackson et al., 2011; Parnell and Jackson, 2013). Only species - age class combinations with $n \geq 4$ in each water mass were included in this analysis.

1.4 Results

1.4.1. Water mass classification

Four water masses were observed in both years (ACW, BCSW, MW, CWW), while Atlantic Water (AW) was observed in 2013 only at a single deep station in Barrow Canyon (Figure 1.1). There was a nearshore-to-offshore gradient of decreasing water temperature with the warmer and fresher ACW nearshore and the relatively cool more saline BCSW offshore. North of approximately 71°N, the surface and bottom waters were cooler (<2°C) and the fresh

and cold MW and cold saline CWW were the dominant water masses. In 2013, the ACW was absent north of 70°N with CWW dominating both nearshore and offshore.

1.4.2. Isoscapes

Calanus spp. baseline isoscapes for both $\delta^{13}C$' and $\delta^{15}N$ showed strong spatial gradients with some differences between 2012 and 2013 (Figure 1.2). Modeled carbon stable isotope values ranged from -24.2‰ to -19.5‰ with similar ranges in both years, although 2013 values were on average enriched in ^{13}C by ~0.8‰. In both years, $\delta^{13}C$' values were highest in BCSW just north of Bering Strait and decreased to the northeast. Nitrogen stable isotope values ranged from 8.0‰ to 10.8‰ over both years, averaging 9.5‰ in 2013 and 10.1‰ in 2012. In both years, the lowest values were observed within and just north of Bering Strait. In 2012, there was also a nearshore-offshore gradient with higher $\delta^{15}N$ values nearshore. In 2013, a similar gradient was observed, but only in the southern part of the study area, with baseline $\delta^{15}N$ values peaking at 162°W and declining further east towards Barrow.

The differences in baseline values explained between 0 and 41% of the variation in unadjusted $\delta^{15}N$ and $\delta^{13}C$' values for each fish species. The baseline variability in $\delta^{15}N$ explained > 20% of the variation in the $\delta^{15}N$ values for hamecon and shorthorn sculpin, while the baseline variability in $\delta^{13}C$' explained > 20% of the variation in the $\delta^{13}C$' values for Arctic cod, capelin, Pacific sandlance, shorthorn sculpin, Bering flounder, slender and stout eelblennies, and Arctic staghorn sculpin. These fishes were collected both demersally and pelagically.

1.4.3. Ontogenetic shifts

For fish samples collected in 2012, mean $\delta^{15}N_{adj}$ values spanned nearly two trophic levels based on a 3.4‰ $\delta^{15}N$ enrichment, with values typically increasing between the age-0 and age1+ groups (Figure 1.3; Tables 1.1, 1.2 and 1.3). Fish collected in the bottom trawl had $\delta^{13}C'_{adj}$ signatures more similar to the Greenland cockle, an epibenthic suspension feeder, whereas the surface trawl caught fish signatures were more similar to *Calanus* spp. Polar eelpout (Lpo) and Arctic staghorn sculpin (Gtr) had the highest mean trophic level, while age-0 Pacific sandlance (Ahe_0) had the lowest value.

For 10 out of the 13 species trophic level ($\delta^{15}N_{adj}$) increased with body length, and the relationship often varied by water mass (Figure 1.4; Table 1.4a). A notable exception was Pacific herring (Cpa) for which trophic level decreased with body length over the observed size range

(Figure 1.4). Modeled trophic levels for walleye pollock (Gch) and capelin (Mvi) dipped at intermediate lengths, though the model for the latter had a very low marginal R^2 of 0.08. For saffron cod (Egr), Bering flounder (Hro), Arctic staghorn sculpin, shorthorn sculpin (Msc), and slender eelblenny (Lfa) trophic level increased most rapidly at shorter lengths (Figure 1.4; Table 1.4a). The relationship with length varied by water mass for 8 out of 13 species (Table 1.4a) with a wider range of $\delta^{15}N_{adj}$ values in the MW/CWW and BCSW than in the ACW (Figure 1.4). In the ACW, model fits overlapped for intermediate sized walleye pollock, Arctic cod, saffron cod and Bering flounder (Figure 1.4).

Similar to $\delta^{15}N_{adj}$, the $\delta^{13}C'_{adj}$ values for 8 out of 13 species increased with ontogeny, indicating a switch from pelagic to benthic prey with size (Figure 1.4; Table 1.4b). The relationship varied by water mass for four species: saffron cod (Egr), Bering flounder (Hro), Arctic staghorn sculpin and stout eelblenny. Several pelagic species (walleye pollock, Pacific sandlance and capelin) showed no trend in $\delta^{13}C'_{adj}$ with ontogeny or differences among water mass structure (Table 1.4b). Though selected models for Arctic cod and Hamecon (Asc) indicated relationship with length and $\delta^{13}C'_{adj}$, the length term explained little of the variability in $\delta^{13}C'_{adj}$ values (Table 1.4b).

Interannual differences were observed in the relationship of $\delta^{15}N_{adj}$ with length for Arctic cod (Figure 1.5), capelin, and Pacific herring and in the mean $\delta^{15}N_{adj}$ for saffron cod (Table 1.5a). All of these species showed consistent enrichment in ^{15}N in 2013 compared with 2012. The difference increased with length for Arctic cod (Figure 1.5) and capelin. Interannual differences were also observed in the relationship of $\delta^{13}C'_{adj}$ with length for Arctic cod (Figure 1.6) and in the mean $\delta^{13}C'_{adj}$ for saffron cod, capelin, and Pacific herring (Table 1.5b). In 2012, saffron cod, capelin and Pacific herring had lower $\delta^{13}C'_{adj}$ values indicative of a more pelagic diet. For several of these species, samples from the 2012 and 2013 surface trawl surveys consisted almost entirely of similar-sized juveniles (Arctic cod, saffron cod, shorthorn sculpin and chum salmon); therefore, detecting ontogenetic shifts over their entire life history was not possible based on these surveys alone. Nevertheless, trends in both $\delta^{15}N_{adj}$ and $\delta^{13}C'_{adj}$ over the available size range were evident for many of these species.

1.4.4 Arctic cod

There was a high degree of overlap in the standard ellipse areas of age-0 Arctic cod between water masses (MW/CWW and BCSW) and between years, moderate overlap between age 1+ Arctic cod from the MW/CWW and from the BCSW within the same year, and almost no overlap of age 1+ Arctic cod between 2012 and 2013 (Figure 1.7). In 2012, it appears that age 1+ Arctic cod fed more pelagically in the BCSW than in the MW/CWW. Furthermore, age 1+ Arctic cod had a more pelagic diet in 2012 than in 2013. Age-0 Arctic cod had similar and overlapping isotopic niche spaces in both years and water masses, indicating a similar diet regardless of year or water mass. Older Arctic cod exhibited a broader isotopic space than age-0 fish. It should be noted that only three age 1+ Arctic cod were sampled for stable isotopes in the BCSW in 2013.

In 2012, regardless of length, Arctic cod sampled in the MW/BCSW, BCSW and BCSW/CWW had the highest C:N values, while cod in MW/CWW had intermediate values and cod in ACW/BCSW and ACW had significantly lower C:N values (Figure 1.8). The best-fit model included a quadratic length term and different intercepts for each water mass structure (marginal R^2=0.33; conditional R^2=0.58). When 2012 and 2013 surface trawl samples were analyzed together, no difference was detected between years or water masses. It should be noted that most of the Arctic cod sampled in the surface trawls were age-0 or age-1 (<12 cm).

1.4.5 Community isotopic space

Fish community isotopic space metrics varied by water mass (Figure 1.9; Table 1.6). The fish community in the ACW had the largest range in $\delta^{13}C'_{adj}$ values (-22.3 to -18.0‰), indicating the highest diversity in basal resources and resulting in the largest total area (isotopic niche space), the largest mean nearest neighbor distances (MNND, lowest redundancy) and the largest distance to the centroid (highest trophic diversity). In contrast, the MW/CWW had a much smaller $\delta^{13}C'_{adj}$ range (-21.3 to -19.2‰), total area (isotopic niche space) and MNND (Figure 1.9; Table 1.6), implying higher trophic redundancy. The fish community in the BCSW fell largely between the other two water masses in terms of the above characteristics, but had the shortest mean distance to the centroid and a $\delta^{13}C'_{adj}$ range from -22.3 to -19.0‰. Based on the lower $\delta^{13}C'_{adj}$ range of fish community in the BCSW, the fishes seem to be relying on more pelagic prey than the fish community in the MW/CWW, which has intermediate values. All three

communities had similar ranges for $\delta^{15}N_{adj}$ (BCSW: 11.6 to 16.1‰; MW/CWW: 11.7 to 16.3‰; ACW: 12.4 to 17.1‰), suggesting that the food chain lengths were similar among communities. However, values in the ACW were slightly higher on average (corresponding to a difference of <0.3 trophic levels).

1.5 Discussion

1.5.1 Isoscapes

Isoscapes revealed temporal and spatial variation in the $\delta^{15}N$ and $\delta^{13}C$' signatures of primary consumers, *Calanus* spp. Isotopic values of primary production have been shown to vary spatially, seasonally and based on species composition (McMahon et al., 2006; Soreide et al., 2006). These differences in baseline isotopic values are linked to nutrient availability (e.g., new [nitrate] vs. regenerated production [ammonium] (Ostrom et al., 1997)), primary productivity (species composition and bloom progression (Soreide et al., 2006; Tamelander et al., 2009)), and microbial degradation (Lovvorn et al., 2005; McTigue et al., 2015; McTigue and Dunton, 2014; North et al., 2014), all of which can be influenced by water mass characteristic and currents.

In both 2012 and 2013 we observed a decline in $\delta^{13}C$' values from the southwest corner of the survey region to the northeastern Chukchi shelf. Similar trends were found in sediment $\delta^{13}C$ values in the northeastern Chukchi Sea (McTigue et al., 2015). The highest $\delta^{13}C$ values were observed in the highly productive Bering Strait region with values decreasing to the northeast. Often, higher $\delta^{13}C$ values are associated with rapid growth rates of phytoplankton (Goericke and Fry, 1994). Generally, $\delta^{13}C$ at the base of the food web decreases with increasing latitude because phytoplankton preferentially uptake $^{12}CO_2$ during photosynthesis and at lower temperatures CO_2 dissolves more readily, increasing the pool of CO_2, which results in a proportionally higher uptake of the lighter $^{12}CO_2$ (reviewed in Fry and Sherr, 1984). In addition, terrestrial carbon tends to be relatively depleted in ^{13}C (Naidu et al., 2000) and $\delta^{13}C$ values were lower along the coast, possibly due to the riverine influence in the Alaska Coastal Current (ACC) (Iken et al., 2010). Similarly, some zooplankton sampled along the coast in the southeast Chukchi Sea (Kotzebue Sound) in the ACW were relatively depleted in $\delta^{13}C$ compared with zooplankton sampled more offshore in the BCSW (Feder et al., 2011). In the present study,

relatively high $\delta^{13}C$' values were observed near Hanna Shoal in 2012, but not in 2013 when the ACC did not extend as far north. The elevated values in 2012 could be due to regeneration of carbon in the relatively stagnant water surrounding Hanna Shoal (Day et al., 2013) or the availability of sea-ice algae, as they tend to be enriched in ^{13}C (Soreide et al., 2006). Regenerated C and N, which has been reworked by microbes, tends to have enriched ^{13}C and variable ^{15}N values (McTigue and Dunton, 2014).

In both 2012 and 2013, baseline $\delta^{15}N$ increased to the northeast although lower values were observed in the far northeastern region in 2013. A previous isotope study in the Bering, Chukchi and Beaufort seas found a similar increase in $\delta^{15}N$ values of planktonic organisms with latitude over a much broader spatial scale, which was attributed to isotopic discrimination and higher nutrient availability in the south (Schell et al., 1998). In the southern Chukchi Sea, Feder et al. (2011) observed larger $\delta^{15}N$ values in copepods in the ACW than farther offshore. The decline in $\delta^{15}N$ values in the northern Chukchi Sea in 2013 may be related to the absence of ACW above 70°N in that year as a result of changes in circulation patterns (Danielson et al., 2017), as the ACW tends to have relatively higher $\delta^{15}N$ values, potentially from nitrogen limitation (Lee et al. 2007).

Natural spatial variations in the isotope values at the base of the food web propagate up to higher trophic levels and need to be accounted for when comparing trophic level of animals over large areas. For example, large-scale spatial differences in $\delta^{15}N$ (ranging from 9.7 to 20.9‰) for yellowfin tuna across the equatorial Pacific and western Indian Oceans were explained by differences in baseline $\delta^{15}N$ values, not diet (Lorrain et al., 2015). In the present study the differences in baseline values explained between 0 and 41% (majority > 20%) of the variation in unadjusted $\delta^{13}C$' values and between 0 and 31% (only 2 species > 20%) of the variation in unadjusted $\delta^{15}N$ values. Likely, the baseline variability explained less of the variation in the $\delta^{15}N$ values than the $\delta^{13}C$' values because there is a large effect of size on $\delta^{15}N$ for most species. In order to account for the natural baseline variability, we had to make several assumptions. Specifically, we assumed that the sampled fishes and the baseline organism *Calanus* spp. have similar turnover rates and movement patterns. Turnover rate, which is the rate of change in tissue isotopic composition based on tissue replacement due to growth and metabolic processes (MacAvoy et al., 2001), tends to vary with organism size and tissue type. For example, smaller fish tend to have faster turnover rates because they typically have higher metabolic and growth

rates (Jennings et al., 2008). The complete isotopic turnover in fish muscle can take anywhere from months (Miller, 2006) to a few years (Hesslein et al., 1993), while shifts in isotopic signatures resulting from diet changes are often observable much sooner. For an Arctic amphipod (Onisimus litoralis) the half-life turnover rate was roughly 20 days (Kaufman et al., 2008) and isotopic changes in Arctic bivalves were evident after 4 weeks (McMahon et al., 2006). Presumably, the turnover rate of calanoid copepods would be similar to or faster than the rates for the larger Arctic amphipods. Therefore, turnover times in the fish consumers, which are typically several months (Miller, 2006), likely do not match the turnover times in their prey. This difference may lead to some error when calculating trophic level or estimating diet source. Moreover, movement patterns may vary, as larger fish may be more mobile or sedentary, while *Calanus* spp. are more subject to currents. This is potentially problematic, especially in regions with steep gradients in baseline isotope values (i.e., the southwest corner in the BCSW for carbon in 2012 and northeast region in the MW/CWW for nitrogen in 2013). Furthermore, baseline ^{15}N values are more depleted in the Bering Sea (Dunton et al., 1989; Schell et al., 1998) and larger fish migrating through Bering Strait into the highly productive Chukchi Sea may have isotopic signatures reflecting their diet in the Bering Sea. Most likely, some of the larger fish have different turnover rates and movement patterns, thus their current isotope signatures may reflect diets at different spatial and time scales. For example, in this study some age 1+ Arctic cod collected in the BCSW had unexpectedly low $\delta^{13}C'_{adj}$ values (lower than the mean *Calanus* spp. values). This is likely due to a temporal or spatial mismatch with the baseline organism.

1.5.2 Trophic roles and ontogenetic shifts

As we hypothesized, the trophic positions of several fish species shifted with ontogeny and often varied with water mass and year. We observed a general increase in trophic level ($\delta^{15}N$) with body size, which has been observed in many ecosystems (Jennings et al., 2002; Marsh et al., 2012; Sherwood and Rose, 2005; Werner and Gilliam, 1984). Typically, as fish grow, their gape size, swimming speed, and energetic demands increase (Scharf et al., 2000). This often leads to consumption of larger, more energy-rich and higher trophic level prey to meet these demands. In addition, fish may change or expand their foraging range as they grow (Werner and Gilliam, 1984). We observed shifts in foraging habitats with increasing length. Typically, younger fish fed in the pelagic zone and increased the proportion of benthic prey as

they grew. However, the pelagic forage fish Pacific sandlance and capelin exhibited only pelagic $\delta^{13}C$' signatures throughout ontogeny.

Several studies have examined fish diets within the eastern Chukchi Sea (Coyle et al., 1997; Edenfield et al., 2011; Frost and Lowry, 1983; Gray et al. 2015, 2017; Iken et al., 2010; Whitehouse et al. 2017) and some have examined ontogenetic diet shifts and regional variability (Coyle et al. 1997; Edenfield et al., 2011; Gray et al. 2015, 2017). Within the Chukchi Sea, Arctic cod, Arctic staghorn sculpin, Bering flounder, shorthorn sculpin and saffron cod are considered generalists that consume a broad range of prey types depending on the local prey available (Coyle et al., 1997; Gray et al., 2017; Whitehouse et al., 2017). In the present study, with the exception of shorthorn sculpin, diet source and trophic level varied by water mass. Similar to the present study, during 1990 and 1991 spatial differences in Arctic cod, Bering flounder and Arctic staghorn sculpin diets were observed between ACW, BCSW and in the MW/CWW (Coyle et al., 1997). Resource partitioning occurs between these species in shared habitats (Coyle et al., 1997; Gray et al. 2017; Whitehouse et al. 2017). However, dietary overlap was observed between similarly sized Arctic and saffron cods (average length roughly 15 cm) collected in the ACW near Point Hope (Coyle et al. 1997). We found that intermediate length Arctic and saffron cods (~10 – 15 cm) sampled in the ACW had nearly identical trophic levels and similar $\delta^{13}C$ values, suggesting a very similar trophic niche and a high potential for competition. In addition to regional dietary differences, shifts with ontogeny have been observed for stout eelblenny, Arctic cod, Arctic staghorn sculpin, Bering flounder and shorthorn sculpin in the northeastern Chukchi Sea (Edenfield et al. 2011; Gray et al. 2015, 2017), which corresponds to increasing trophic levels and increasing importance of benthic prey items with length in the current study.

1.5.3 Arctic cod

Trophic level, diet and body condition of Arctic cod (C:N) varied with body length, water mass and year for Arctic cod. Age-0 Arctic cod occupied a similar isotopic niche space in different water masses, while larger Arctic cod consumed a broader diet of higher trophic level prey that varied by water mass. Our results are consistent with stomach content studies that examined diet over a shorter time scale. Arctic cod are considered generalist zooplanktivores, with diet reflecting local prey availability (Bradstreet et al., 1986). In addition to varying with

time and location, Arctic cod diets have been observed to vary with body size (Coyle et al., 1997; Cui et al., 2012; Edenfield et al., 2011; Gray et al., 2015; Rand et al., 2013). In the northeastern Chukchi Sea, age-0 Arctic cod exclusively consumed small, pelagic prey, mainly calanoid copepods (Gray et al., 2015). Similarly, small Arctic cod (7 – 11 cm) in the northern Bering Sea occupied a narrow niche feeding mainly on copepods, while larger Arctic cod (14 – 22 cm) had a broader dietary niche (Cui et al., 2012). In the northeastern Chukchi Sea, diets of larger Arctic cod (> 7 cm) had a higher proportion of benthic prey compared with smaller Arctic cod (≤ 7 cm), though pelagic zooplankton remained the primary food (Gray et al., 2015). In the present study we found Arctic cod to expand their foraging range as they grow and consume higher trophic level prey, but this varied by water mass. In 2012, age 1+ Arctic cod in the BCSW fed mainly on pelagic prey, while cod in the MW/CWW incorporated more benthic prey. Moreover, we found significantly higher C:N values in cod from nutrient-rich BCSW than in cod from the nutrient-poor ACW, with relatively low zooplankton densities. This pattern in C:N ratios likely indicates a diet of lipid-rich *Calanus* spp. in the BCSW. The difference between water masses corresponds to a diet study in the early 1990s in the Chukchi Sea, in which Arctic cod collected in the ACW had no *Calanus* spp. in their stomachs, while the energy dense *Calanus* spp. were the dominant prey for Arctic cod collected in the BCSW (Coyle et al., 1997). Similarly, Arctic cod has higher energy densities offshore and near Barrow Canyon, as opposed to nearshore in the ACW (J. Vollenweider, pers. comm.). We hypothesize that fish in offshore waters (BCSW and MW) may have an advantage over those in coastal waters in terms of prey quality or quantity if higher energetic values reflect the ability to allocate energy to lipid storage.

Differences in the spatial extent of Pacific water masses in the Chukchi Sea between 2013 and 2012 may explain higher $\delta^{13}C'_{adj}$ and $\delta^{15}N_{adj}$ values of age-1+ Arctic cod in 2013 than 2012, indicating a more benthic diet in 2013. Specifically, ACW and BCSW in 2013 did not extend as far north on the NE Chukchi shelf and these waters were colder, fresher and had fewer nutrients on average to support pelagic production, possibly reflecting less inflow through Bering Strait (Danielson et al., 2017). Reduced advection into the Chukchi Sea, lower temperatures and/or less nutrients, in turn, may have resulted in lower densities of *Calanus* spp. observed in 2013, especially in the northern half of the survey area (Pinchuk and Eisner, 2017). Because of this lack of suitable pelagic prey, Arctic cod may have relied more on benthic prey resulting in higher observed $\delta^{13}C'_{adj}$ and $\delta^{15}N_{adj}$ values.

1.5.4 Isotopic niche space

In addition to spatial variation in intraspecific trophic positions, regional variation in the isotopic niche space of the fish communities suggests differences in food web structure among water masses. Observed differences in isotopic niche space between water masses appear to be a combination of fish species composition and prey availability. Fewer fish species were sampled in the colder MW/CWW. A narrower prey base was observed in the Arctic MW/CWW with intermediate $\delta^{13}C'_{adj}$ values, which suggests a higher reliance on benthic prey and corresponds to a high benthic biomass surrounding Barrow Canyon (Fox et al., 2014; Grebmeier, 2012; Grebmeier et al., 2006). The isotopic turnover rates for fish muscle tissues integrate diet over the past few months (Miller, 2006), so the stable isotope signatures from fishes collected in the MW/CWW may reflect diets of fishes during a time preceding ice-retreat. During ice-cover, fishes within this region may have been largely limited to benthic or ice-associated prey. A more pelagic resource base (lower $\delta^{13}C'_{adj}$) was observed in the BCSW, which is known for high primary and secondary productivity in the water column. These results support previous studies delineating two separate ecosystems with different food web structures in the northeastern Chukchi Sea: a pelagic dominated system in the BCSW and a more benthic driven ecosystem in the MW/CWW (Day et al., 2013).

Fish communities and species with higher resilience are more likely to withstand disturbances resulting from climate change. Community resilience depends on functional redundancy (multiple species with a similar niche space), complexity (many species, many trophic linkages) and resource availability (nutrients and primary production) (Blanchard et al., 2011; Rice et al., 2013; Rosenfeld, 2002). As previously mentioned, in the Chukchi Sea resource and nutrient availability is linked to oceanographic processes, including waters advected through Bering Strait. It is unknown how flow through Bering Strait might change under climate warming, but the Chukchi Sea on the whole may become more like the present-day Bering Sea shelf (earlier ice-retreat, more pelagic system). Warmer and fresher waters may favor smaller phytoplankton that are more likely to be retained in the surface waters (Li et al., 2009). Also, the warmer water may enhance zooplankton growth and reproduction. Smaller phytoplankton and enhanced grazing pressures would presumably weaken benthic-pelagic coupling. The Arctic fish community in the MW/CWW had the smallest isotopic niche space (lowest complexity and trophic diversity), a limited resource base, but a slightly higher trophic redundancy. On the other

hand, the BCSW community draws on a broader resource base and had over twice the isotopic niche space and higher trophic diversity. This seems to imply a competitive advantage and when the Bering Sea influence is larger (i.e., BCSW extends farther north), the community associated with this water mass may displace the species-poor Arctic fish community. Central to the Arctic community is the Arctic cod, which was present in all water masses and showed some diet adaptability, indicating some resilience to ecosystem changes. However, age-0 Arctic cod occupied a narrow isotopic niche space and did not occur in the ACW, indicating that they are more vulnerable than adults to a changing prey field that might result from a changing climate. Limited accessibility due to remoteness, seasonal ice cover and the high costs of sampling have until recently limited the number of surveys in the Chukchi Sea, an extremely dynamic region experiencing pronounced climate warming (Wang et al., 2013). Although numerous studies have sampled demersal fishes in the Chukchi Sea over recent decades (Norcross et al 2010), this was the first spatially comprehensive, synoptic fisheries oceanographic survey across water masses in the US portion of the Chukchi Sea. As such, this project provides a benchmark for isotopic values of key demersal and pelagic fish species throughout the eastern Chukchi shelf. Against this benchmark, future changes in response to climate warming and anthropogenic activities (e.g., oil exploration, shipping, fisheries, tourism) can be monitored. For many of the fish species in the Chukchi Sea, we demonstrated that diet varies with body-length, region (water mass) and year. Our estimates of trophic levels and energy pathways for common fish species in the Chukchi Sea can also inform food web models, such as the Ecopath model developed at the Alaska Fisheries Science Center (Whitehouse et al., 2014).

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Table 1.1. Fish and invertebrate samples collected for stable isotope analysis during the 2012 surface trawl survey in the eastern Chukchi Sea by age class (age-0, age-1+, mature fish (Mat) or juvenile salmon (Juv)), including sample size (N), species/age abbreviation code, fork length range (cm), average raw $\delta^{15}N \pm$ SD (‰), average $\delta^{15}N_{adj} \pm$ SD (‰), trophic level (TL), average raw $\delta^{13}C \pm$ SD (‰), average lipid-normalized $\delta^{13}C' \pm$ SD (‰), and average $\delta^{13}C'_{adj} \pm$ SD (‰).

			Surface 2012							
Species (Common name)	Age	Code	N	Size range	$\delta^{15}N$ (SD)	$\delta^{15}N_{adj}$ (SD)	TL	$\delta^{13}C$ (SD)	$\delta^{13}C'$ (SD)	$\delta^{13}C'_{adj}$ (SD)
Boreogadus saida (Arctic cod)	0	Bsa_0	79	3.4 – 6.0	12.8 (0.6)	12.6 (0.4)	2.7	-21.4 (0.8)	-21.3 (0.7)	-20.8 (0.7)
	1+	Bsa	47	6.6 – 13.5	13.9 (0.6)	13.9 (0.8)	3.1	-20.6 (1.0)	-20.6 (1.0)	-20.7 (1.3)
Eliginus gracilis (Saffron cod)	0	Egr_0	40	3.2 – 5.9	12.8 (0.6)	12.7 (0.6)	2.7	-21.2 (0.6)	-21.2 (0.6)	-21.0 (0.7)
	1+	Egr	18	6.9 – 13.9	14.9 (0.4)	15.3 (0.6)	3.6	-20.0 (0.8)	-20.1 (0.8)	-20.7 (0.9)
Gadus chalcogrammus (Walleye pollock)	1+	Gch	15	9.4 – 12.3	14.1 (0.3)	15.0 (0.5)	3.4	-20.7 (0.3)	-20.8 (0.3)	-22.4 (0.9)
Myoxocephalus scorpius (Shorthorn sculpin)	0	Msc_0	18	3.2 – 4.7	13.3 (0.9)	12.7 (0.7)	2.9	-19.8 (0.6)	-19.8 (0.6)	-20.0 (0.7)
	1+	Msc	10	6.5 – 15.3	15.4 (0.9)	15.4 (1.0)	3.6	-19.6 (0.8)	-19.9 (0.7)	-20.0 (1.0)
Mallotus villosus (Capelin)	0	Mvi_0	26	4.4 – 7.5	13.8 (0.7)	13.7 (0.9)	3.1	-21.4 (0.5)	-21.3 (0.6)	-20.9 (1.0)
	1+	Mvi	77	7.6 – 13.1	13.4 (0.8)	13.6 (0.9)	3.0	-20.8 (0.8)	-20.7 (0.9)	-20.9 (1.3)
Clupea pallisii (Pacific herring)	Mat	Cpa	46	19.1 – 31.3	14.4 (0.6)	14.9 (0.7)	3.4	-21.4 (0.9)	-20.9 (0.7)	-22.0 (1.1)
Ammodytes hexapterus (Pacific sandlance)	0	Ahe_0	50	3.6 – 7.0	11.6 (0.7)	11.6 (0.6)	2.4	-21.8 (0.6)	-21.3 (0.6)	-20.8 (0.7)
	1+	Ahe	37	7.2 – 16.1	13.1 (0.7)	13.3 (0.9)	3.0	-21.9 (0.9)	-21.6 (0.8)	-22.0 (0.8)
Oncorhynchus keta (Chum salmon)	Juv	Oke	30	9.1 – 15.1	13.7 (0.6)	14.0 (1.0)	3.1	-21.4 (0.5)	-21.5 (0.6)	-22.3 (1.2)
Calanus spp. (Copepod)	--	Cal	135	--	10.1 (0.7)	--	2.0	--	-23.2 (1.3)	-22.9 (1.2)

Table 1.2. Fish and invertebrate samples collected for stable isotope analysis during the 2013 surface trawl survey in the eastern Chukchi Sea by age class (age-0, age-1+, mature fish (Mat) or juvenile salmon (Juv)), including sample size (N), species/age abbreviation code, fork length range (cm), average raw $\delta^{15}N \pm$ SD (‰), average $\delta^{15}N_{adj} \pm$ SD (‰), trophic level (TL), average raw $\delta^{13}C \pm$ SD (‰), average lipid-normalized $\delta^{13}C' \pm$ SD (‰), and average $\delta^{13}C'_{adj} \pm$ SD (‰).

		Surface 2013							
Species (Common name)	Age	N	Size range	$\delta^{15}N$ (SD)	$\delta^{15}N_{adj}$ (SD)	TL	$\delta^{13}C$ (SD)	$\delta^{13}C'$ (SD)	$\delta^{13}C'_{adj}$ (SD)
Boreogadus saida (Arctic cod)	0	123	2.7 – 5.8	12.1 (1.0)	12.0 (1.0)	2.7	-20.4 (0.9)	-20.2 (0.9)	-20.0 (0.6)
	1+	57	6.2 – 17.4	14.5 (1.0)	14.6 (1.0)	3.5	-20.1 (0.6)	-20.1 (0.6)	-18.8 (0.7)
Eliginus gracilis (Saffron cod)	0	32	3.3 – 5.8	13.3 (0.5)	13.4 (0.9)	3.1	-20.9 (0.8)	-21.0 (0.9)	-21.8 (1.3)
Gadus chalcogrammus (Walleye pollock)	1+	2	9.0 – 10.8	15.1 (1.1)	15.8 (1.7)	3.8	-19.4 (0.6)	-19.5 (0.5)	-20.8 (0.7)
Myoxocephalus scorpius (Shorthorn sculpin)	0	50	2.6 – 5.2	12.9 (1.1)	12.8 (0.8)	3	-19.3 (0.9)	-19.2 (1.1)	-19.8 (0.8)
Mallotus villosus (Capelin)	0	39	4.2 – 7.3	13.9 (1.0)	13.8 (1.2)	3.3	-21.6 (0.7)	-21.9 (1.0)	-21.2 (0.9)
	1+	58	7.4 – 12.5	13.9 (0.7)	13.8 (1.0)	3.3	-20.3 (0.6)	-20.4 (0.6)	-20.7 (0.9)
Clupea pallisii (Pacific herring)	Mat	36	21.1 – 27.4	15.0 (0.8)	15.4 (1.2)	3.7	-22.1 (0.9)	-21.7 (1.1)	-22.6 (1.2)
Ammodytes hexapterus (Pacific sandlance)	0	54	3.4 – 6.8	11.3 (0.8)	10.9 (0.9)	2.4	-21.6 (0.9)	-21.1 (1.0)	-20.6 (0.8)
	1+	30	6.9 – 15.5	13.1 (0.8)	12.9 (1.0)	3	-20.5 (0.5)	-20.4 (0.6)	-20.7 (0.9)
Oncorhynchus keta (Chum salmon)	Juv	30	11 – 15.4	13.5 (0.9)	13.3 (1.1)	3.1	-20.9 (0.5)	-20.8 (0.3)	-21.7 (0.5)
O. gorbuscha (Pink salmon)	Juv	30	8.1 – 14.0	12.7 (1.2)	13.1 (1.7)	3.1	-20.9 (0.6)	-20.6 (0.7)	-21.8 (1.1)
Calanus spp. (Copepod)	--	146	--	9.3 (1.1)	9.5 (1.2)	2	-22.8 (1.4)	-22.1 (1.3)	-22.2 (1.4)

Table 1.3. Fish and invertebrate samples collected for stable isotope analysis during the 2012 bottom trawl survey of the eastern Chukchi Sea by age class (age-0 and age-1+), including species/age abbreviation code, sample size (N), fork length range (cm), average raw $\delta^{15}N \pm$ SD (‰), average $\delta^{15}N_{adj} \pm$ SD (‰), and average $\delta^{13}C'_{adj} \pm$ SD (‰).

Species (Common name)	Age	Code	N	Size range	$\delta^{15}N$ (SD)	$\delta^{15}N_{adj}$ (SD)	TL	$\delta^{13}C$ (SD)	$\delta^{13}C'$ (SD)	$\delta^{13}C'_{adj}$ (SD)
Boreogadus saida	0	Bsa_0	13	4 – 6.1	12.6 (0.6)	12.5 (0.6)	2.7	-20.8 (1.1)	-20.6 (0.9)	-20.5 (0.8)
(Arctic cod)	1+	Bsa	195	6.3 – 21.2	14.4 (1.0)	14.6 (0.9)	3.3	-20.4 (0.6)	-20.5 (0.7)	-21.0 (1.2)
Eliginus gracilis	0	Egr_0	24	3.9 – 6.0	13.2 (0.5)	12.9 (0.5)	2.8	-21.2 (0.7)	-21.2 (0.7)	-21.2 (0.7)
(Saffron cod)	1+	Egr	87	6.1 – 36.0	15.5 (0.8)	15.6 (1.0)	3.6	-19.4 (0.9)	-19.6 (0.9)	-20.0 (1.1)
Gadus chalcogrammus (Walleye pollock)	1+	Gch	29	7.4 – 14.6	14.2 (0.6)	14.0 (0.6)	3.2	-21.1 (0.5)	-21.2 (0.5)	-20.6 (0.8)
Myoxocephalus scorpius	0	Msc_0	6	3.9 – 4.8	13.2 (0.7)	13.0 (0.7)	2.8	-19.5 (0.3)	-20.0 (0.3)	-20.2 (0.3)
(Shorthorn sculpin)	1+	Msc	4	7.1 – 17.8	15.1 (0.6)	14.9 (0.8)	3.4	-19.2 (0.7)	-19.6 (0.7)	-19.4 (0.7)
Hippoglossoides robustus	0	Hro_0	35	3.1 – 6.9	13.8 (1.4)	13.8 (1.5)	3.1	-20.6 (0.9)	-20.8 (0.8)	-20.6 (0.9)
(Bering flounder)	1+	Hro	42	8.2 – 24.8	15.5 (1.3)	15.6 (1.2)	3.6	-19.0 (1.1)	-19.3 (1.2)	-19.7 (0.8)
Anisarchus medius	0	Ame_0	26	5.7 – 7.0	13.7 (0.7)	13.9 (0.7)	3.1	-20.6 (1.1)	-20.7 (1.2)	-20.6 (1.3)
(Stout eelblenny)	1+	Ame	48	7.2 – 15.6	15.2 (1.1)	15.4 (0.9)	3.6	-18.9 (1.0)	-19.2 (1.0)	-19.8 (1.0)
Lumpenus fabricii	0	Lfa_0	25	5.5 – 6.9	13.5 (0.9)	13.3 (0.9)	2.9	-21.1 (0.9)	-21.0 (0.9)	-20.6 (0.8)
(Slender eelblenny)	1+	Lfa	54	7.2 – 27.0	14.6 (1.4)	14.9 (1.1)	3.4	-19.0 (1.1)	-19.1 (1.1)	-19.6 (1.3)
Stichaeus punctatus	0	Spu_0	16	3.3 – 6.2	13.9 (0.6)	13.6 (0.6)	3.0	-19.9 (0.6)	-19.8 (0.6)	-19.8 (0.7)
(Arctic shanny)	1+	Spu	19	6.8 – 14.0	14.7 (0.8)	14.6 (0.8)	3.3	-19.1 (0.5)	-19.1 (0.5)	-19.2 (0.7)
Lycodes polaris (Polar eelpout)	All	Lpo	13	6.6 – 26.1	16.5 (0.7)	16.8 (0.8)	4.0	-18.8 (1.0)	-18.8 (0.9)	-19.3 (1.1)
Artediellus scaber	0	Asc_0	34	3.2 – 5.7	14.4 (1.1)	14.2 (0.9)	3.2	-19.1 (0.7)	-19.1 (0.7)	-19.0 (0.7)
(Hamecon)	1+	Asc	51	5.8 – 9.0	15.3 (1.1)	15.1 (1.0)	3.5	-18.7 (0.9)	-18.8 (0.9)	-18.4 (0.8)
Gymnocanthus tricuspis	0	Gtr_0	28	3.0 – 6.1	14.1 (1.4)	14.0 (1.6)	3.2	-20.3 (1.1)	-20.2 (1.0)	-20.3 (0.7)
(Arctic staghorn sculpin)	1+	Gtr	59	6.5 – 17.0	16.1 (0.9)	16.1 (0.8)	3.8	-19.0 (1.1)	-19.0 (1.1)	-19.3 (1.0)
Serripes groenlandicus (Greenland cockle)		Sgr	28	--	10.0 (0.5)	--	2.0	-19.1 (0.8)	-18.4 (0.6)	--

Table 1.4. Best-fit models with random effects structure (none, random intercept, or random intercept and slope) and resulting R^2 values for species-specific ontogenetic shifts in $\delta^{15}N_{adj}$ (A) and $\delta^{13}C'_{adj}$ (B) with water mass (combined 2012 surface and bottom trawl samples only). Also, p-values from likelihood ratio tests comparing each best-fit model with the corresponding intercept-only model (null model) with the same random effects structure are shown. Models tested include quadratic (Q(L)), log-linear (ln(L)) and linear (L) length terms with additive (+) or multiplicative (*, i.e. including an interaction term) effects of water mass (w). See methods for details. Only fish species that occurred in multiple water masses with adequate numbers were included in analysis. Bolded species model fits are shown in Figure 1.4.

A) Common name	Code	Best-fit model	Random effects	Marginal R^2	Conditional R^2	p-value
Arctic cod	Bsa	L * w	intercept	0.78	0.81	<0.0001
Saffron cod	Egr	ln(L) * w	intercept	0.68	0.91	<0.0001
Capelin	Mvi	Q(L)	intercept	0.08	0.72	0.0001
Pacific sandlance	Ahe	ln(L) + w	none	0.80*	--	<0.0001
Pacific herring	Cpa	L	intercept	0.23	0.71	<0.0001
Bering flounder	Hro	ln(L) + w	intercept	0.57	0.75	<0.0001
Arctic staghorn sculpin	Gtr	ln(L) * w	intercept	0.57	0.88	<0.0001
Shorthorn sculpin	Msc	ln(L)	intercept	0.59	0.91	<0.0001
Slender eelblenny	Lfa	ln(L)	intercept	0.18	0.76	<0.0001
Stout eelblenny	Ame	L * w	none	0.67*	--	<0.0001
Walleye pollock	Gch	Q(L) * w	intercept	0.28	0.8	<0.0001
Arctic shanny	Spu	L	none	0.44*	--	<0.0001
Hamecon	Asc	L + w	intercept	0.39	0.77	<0.0001

B) Common name	Code	Best-fit model	Random effects	Marginal R^2	Conditional R^2	p-value
Arctic cod	Bsa	Q(L)	intercept	0.01	0.75	0.02
Saffron cod	Egr	Q(L) * w	intercept	0.50	0.85	<0.0001
Capelin	Mvi	null	intercept	0.00	0.79	NA
Pacific sandlance	Ahe	null	intercept	0.00	0.68	NA
Pacific herring	Cpa	Q(L)	intercept	0.23	0.92	<0.0001
Bering Flounder	Hro	ln(L) + w	intercept	0.46	0.67	<0.0001
Arctic staghorn sculpin	Gtr	L + w	none	0.39*	--	<0.0001
Shorthorn sculpin	Msc	ln(L)	intercept	0.22	0.57	<0.0001
Slender eelblenny	Lfa	Q(L)	intercept	0.27	0.62	<0.0001
Stout eelblenny	Ame	Q(L) * w	intercept	0.45	0.82	<0.0001
Walleye pollock	Gch	null	intercept	0.00	0.84	NA
Arctic shanny	Spu	ln(L)	none	0.46*	--	<0.0001
Hamecon	Asc	Q(L)	intercept	0.03	0.93	0.02

*adjusted R^2 from simple linear regression model

Table 1.5. Best-fit models with random effects structure (none, random intercept or random intercept and slope) and resulting R^2 values for species-specific ontogenetic shifts in $\delta^{15}N_{adj}$ (A) and $\delta^{13}C'_{adj}$ (B) with water mass and year (combined 2012 and 2013 surface trawl samples only). Also shown are p-values from a likelihood ratio test comparing each best-fit model with the corresponding intercept-only model (null model) with the same random effects. Models tested include quadratic (Q(L)), log-linear (ln(L)) or linear (L) length terms with additive (+) or multiplicative (*, i.e. including an interaction term) effects of water mass (w) and/or year (y). See methods for details. Model fits are shown in Figure 1.4.

A) Common name	Best-fit model	Random effects	Marginal R^2	Conditional R^2	p-value
Arctic cod	ln(L) * y	intercept	0.44	0.71	<0.0001
Pacific sandlance	L + w	intercept	0.63	0.84	<0.0001
Saffron cod	ln(L) + y	intercept	0.48	0.91	<0.0001
Capelin	Q(L) * y	intercept	0.28	0.80	<0.0001
Chum	ln(L)	intercept	0.09	0.75	0.0007
Shorthorn sculpin	ln(L)	intercept	0.47	0.51	<0.0001
Pacific herring	Q(L) * y	intercept	0.35	0.79	<0.0001
B) Common name	Best-fit model	Random effects	Marginal R^2	Conditional R^2	p-value
Arctic cod	Q(L) * y	intercept	0.21	0.52	<0.0001
Pacific sandlance	w	intercept	0.17	0.58	0.02
Saffron cod	L + y + w	intercept	0.66	0.91	<0.0001
Capelin	ln(L) + y	intercept	0.25	0.75	<0.0001
Chum	Q(L)	intercept	0.02	0.89	0.04
Shorthorn sculpin	ln(L) + w	none	0.23*	--	0.0006
Pacific herring	Q(L) + y	intercept	0.48	0.82	<0.0001

*adjusted R^2 from simple linear regression model

Table 1.6. Isotope niche fish community metrics (Layman et al. 2007) by water mass. Metrics shown are total area, $\delta^{15}N$ range, $\delta^{15}C$ range, mean distance to centroid (CD), mean nearest neighbor distance (MNND) and standard deviation of nearest neighbor distance (SDNND). Water mass structures listed are Alaska Coastal Water (ACW), Bering Chukchi Summer Water (BCSW) and Melt Water over Chukchi Winter Water (MW/CWW).

Water Mass	Total Area	$\delta^{15}N$ Range (‰)	$\delta^{13}C$ Range (‰)	CD	MNND	SDNND
ACW	11.3	4.7	4.3	1.46	0.60	0.32
BCSW	8.8	4.4	3.3	1.28	0.50	0.32
MW/CWW	4.3	4.6	2.1	1.34	0.38	0.25

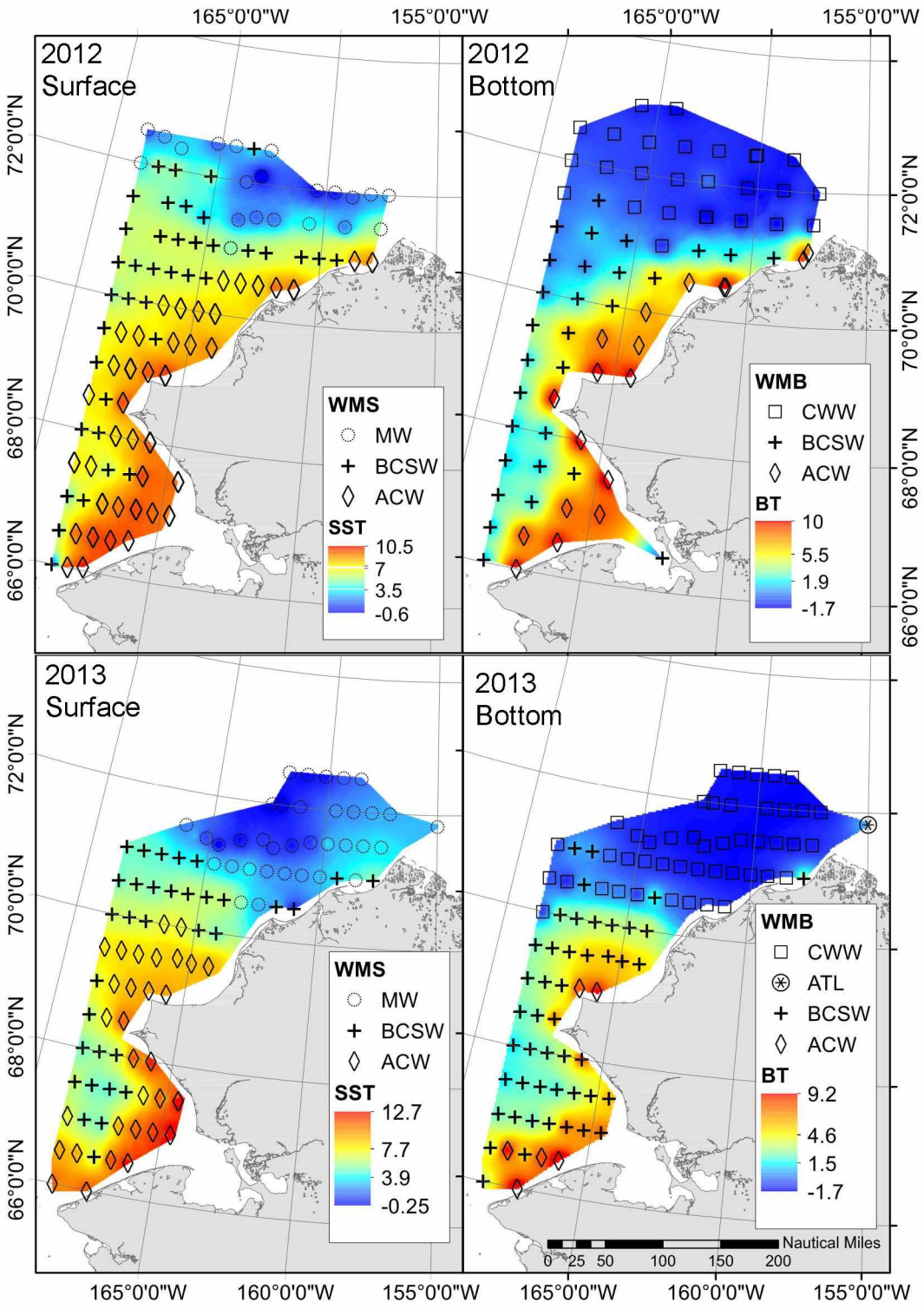

Figure 1.1. Station locations in 2012 (top) and 2013 (bottom) with near surface (left) and near bottom (right) water temperatures and surface water mass classifications (MW = Melt Water, BCSW = Bering Chukchi Summer Water and ACW = Alaska Coastal Water) and near bottom (right) water temperatures and bottom water mass classifications (CWW = Chukchi Winter Water, ATL = Atlantic Water, BCSW and ACW). Temperatures were interpolated using inverse distance weighting tool in ArcGIS 10.1.

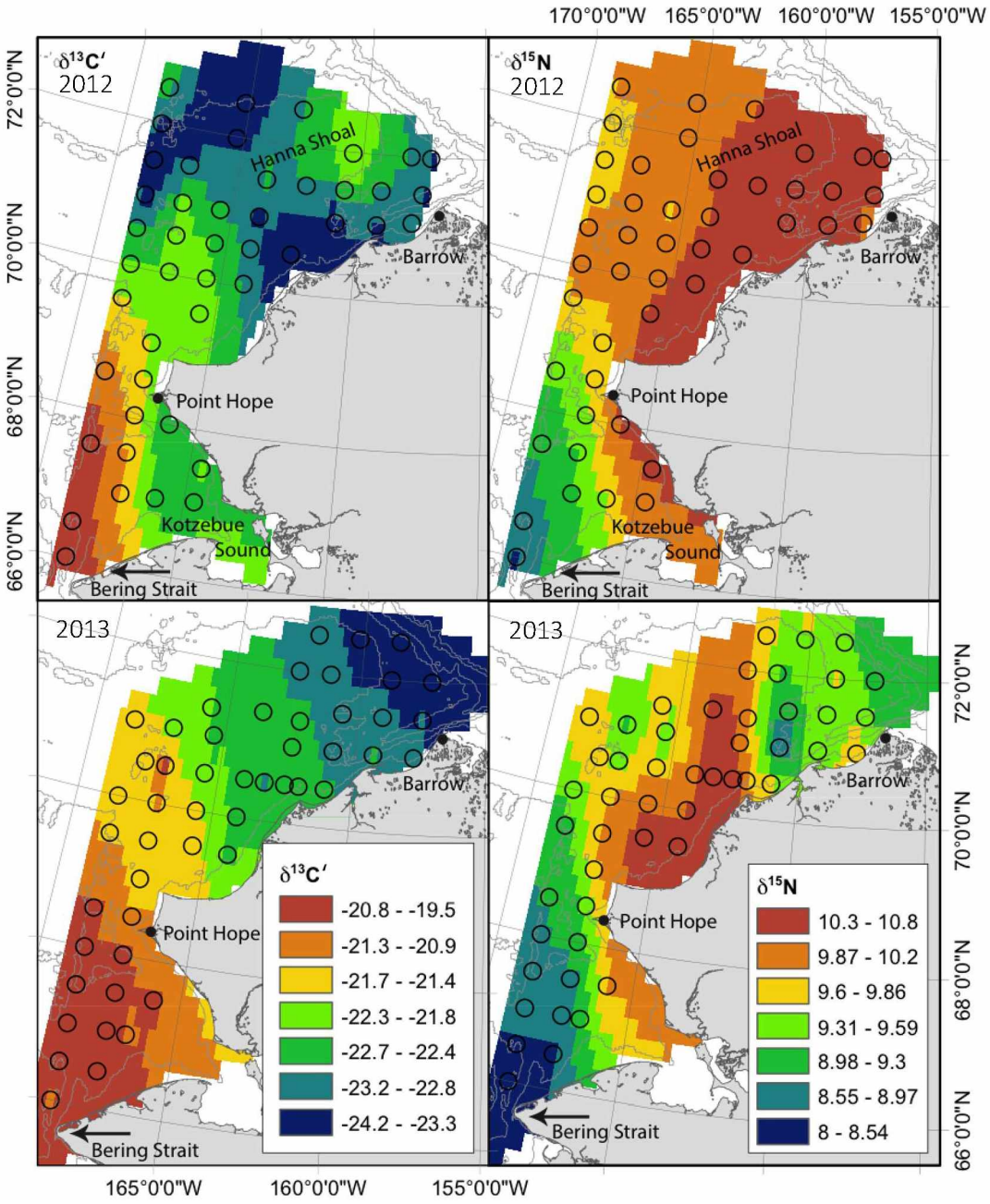

Figure 1.2. 2012 (top) and 2013 (bottom) *Calanus* spp. $\delta^{13}C'$ (left) and $\delta^{15}N$ (right) isoscapes. *Calanus* spp. sampling locations are shown with open circles.

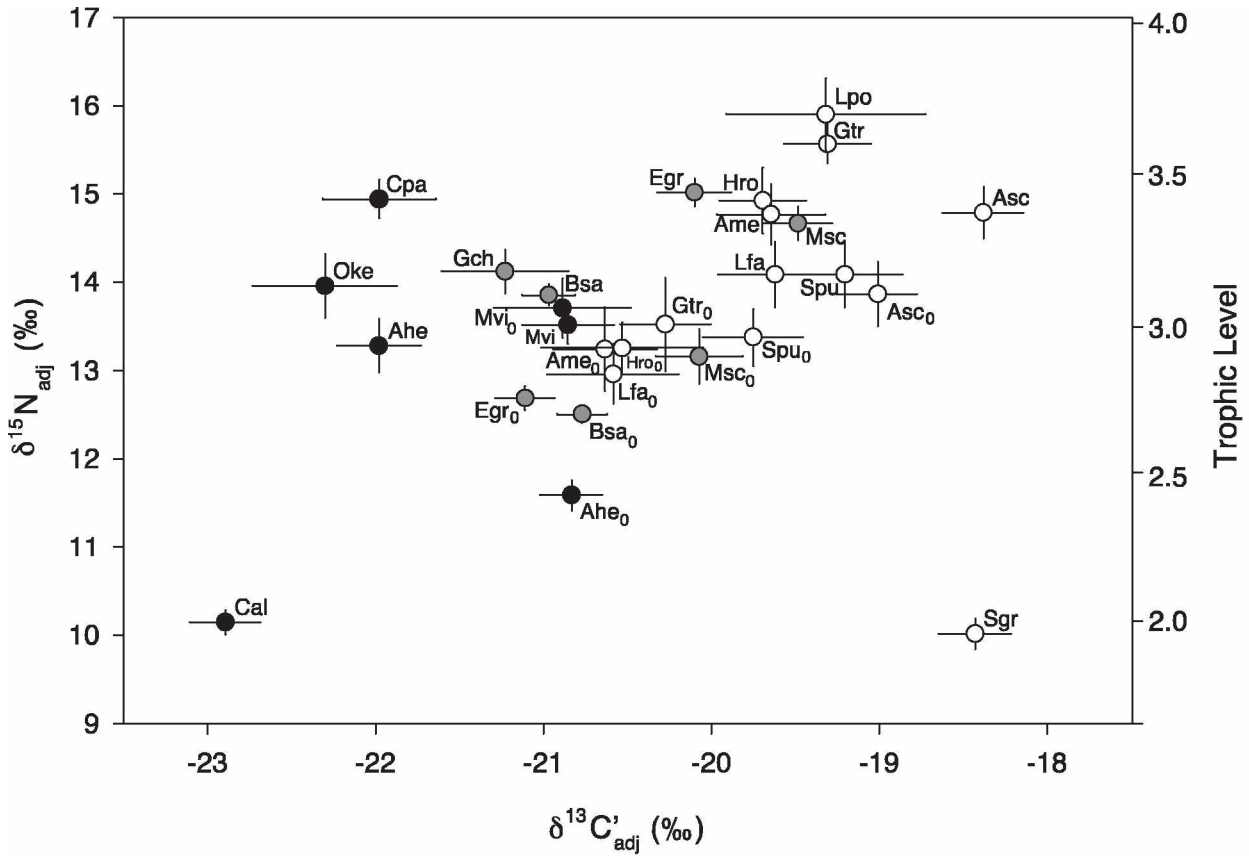

Figure 1.3. Overall 2012 mean carbon isotope values (± 2 SE) and mean nitrogen isotope values (± 2 SE) for each species by age group (age-0 with subscript '0' and/or age-1+ without subscript) in the eastern Chukchi Sea. Species collected during the bottom trawl survey only are shown with open circles, species collected during the surface trawl survey only are shown with black circles and species collected during both surveys are shown in gray. For species codes, see Tables 1.1 and 1.3.

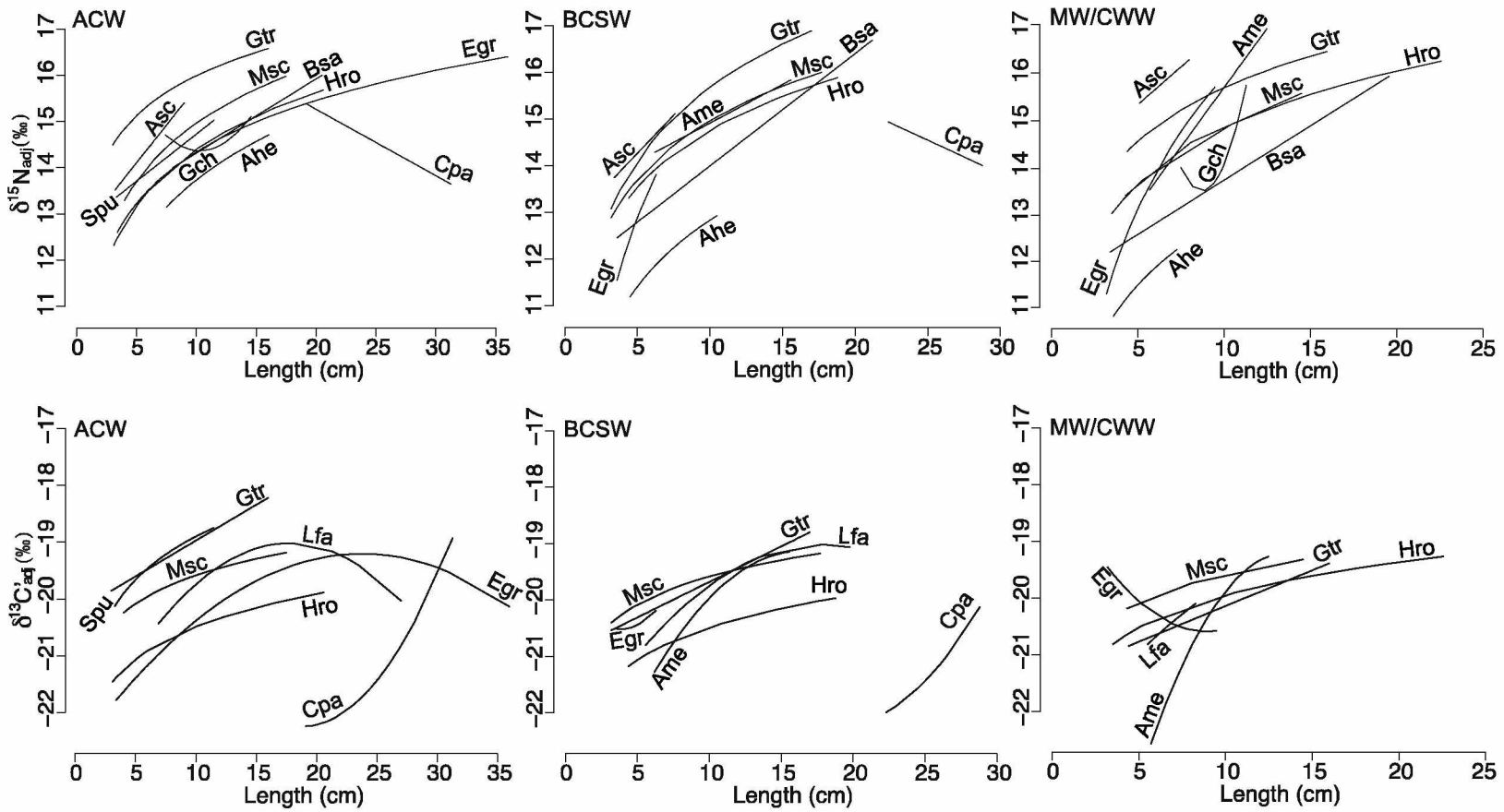

Figure 1.4. Modeled relationships between $\delta^{15}N_{adj}$ (top row) or $\delta^{13}C'_{adj}$ (bottom) and fork length for each species by water mass showing ontogenetic shifts in trophic level and feeding habitat/ diet source, respectively, based on 2012 samples. Water masses shown are Alaska Coastal Water (ACW), Bering Chukchi Summer Water (BCSW) and Melt Water over Chukchi Winter Water (MW/CWW). See tables 1.1 and 1.3 for species codes and Table 1.4 for corresponding best-fit models. Walleye pollock, Pacific sandlance, Arctic cod, and capelin showed no trends in $\delta^{13}C'_{adj}$ with ontogeny or differences among water masses, and are not shown.

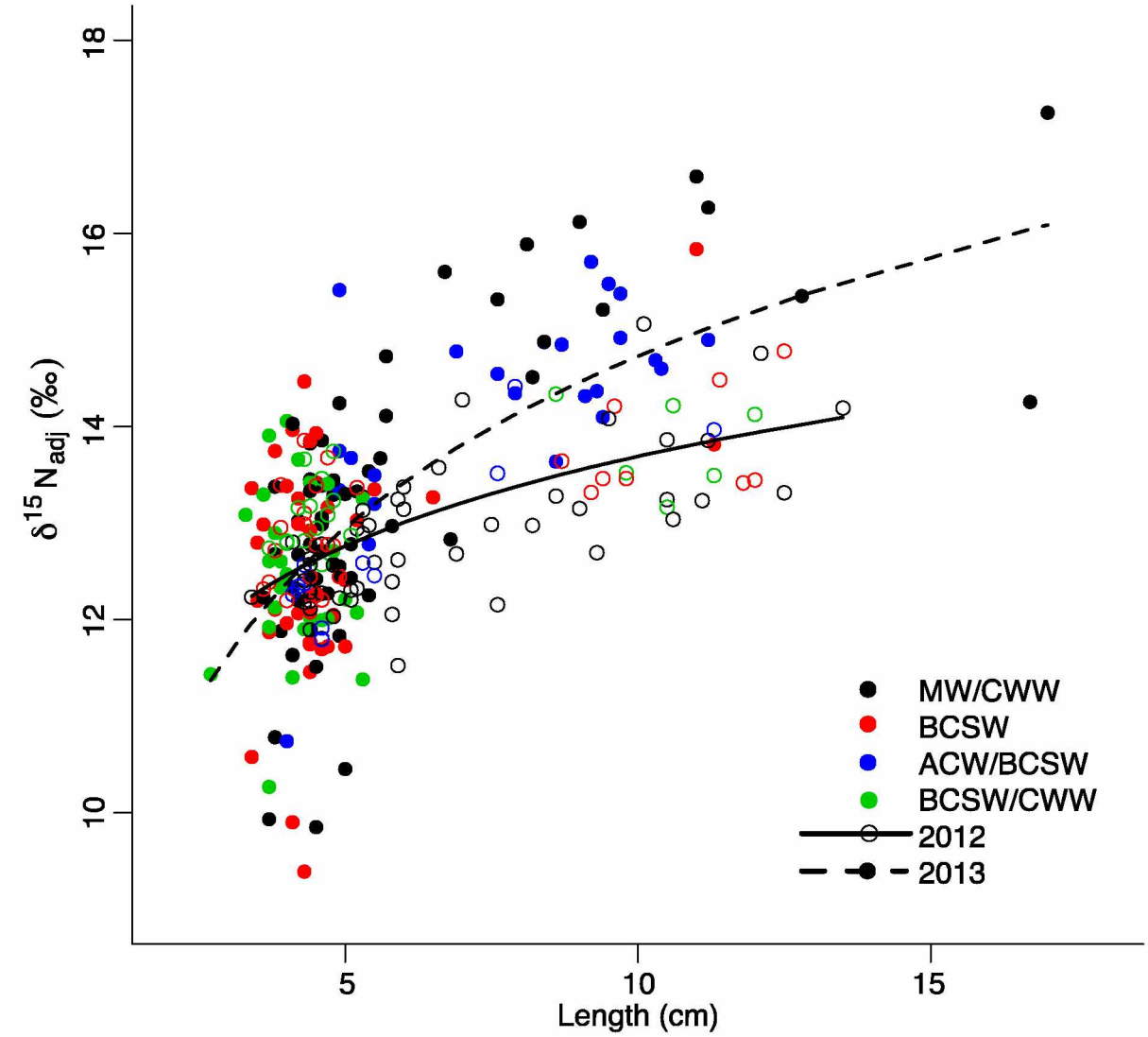

Figure 1.5. Modeled relationships between $\delta^{15}N_{adj}$ and fork length for Arctic cod by year (surface trawl only). See Figure 1.4 for water mass abbreviations.

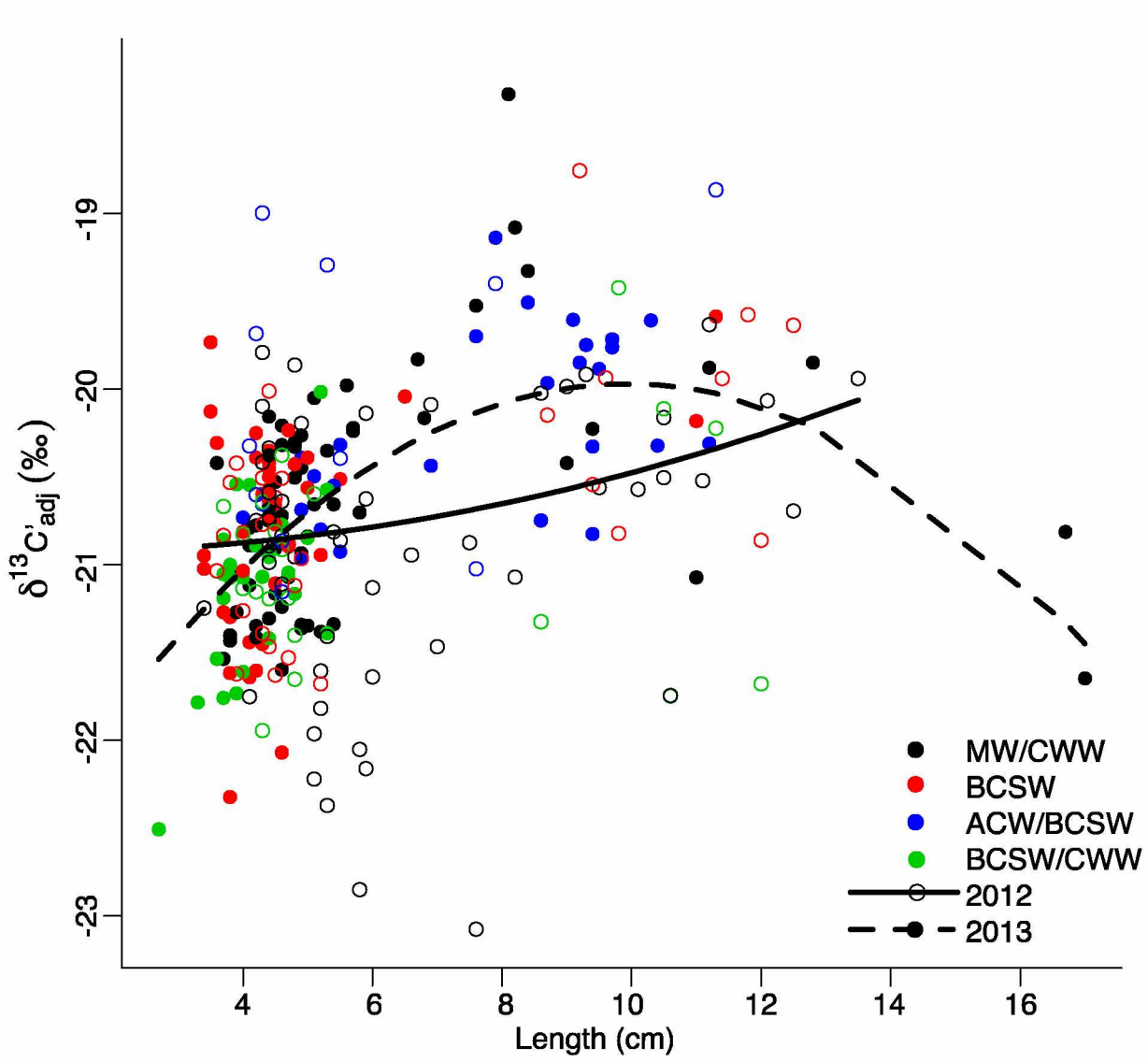

Figure 1.6. Modeled relationships between $\delta^{13}C'_{adj}$ and fork length for Arctic cod by year (surface trawl only). See Figure 1.4 for water mass abbreviations.

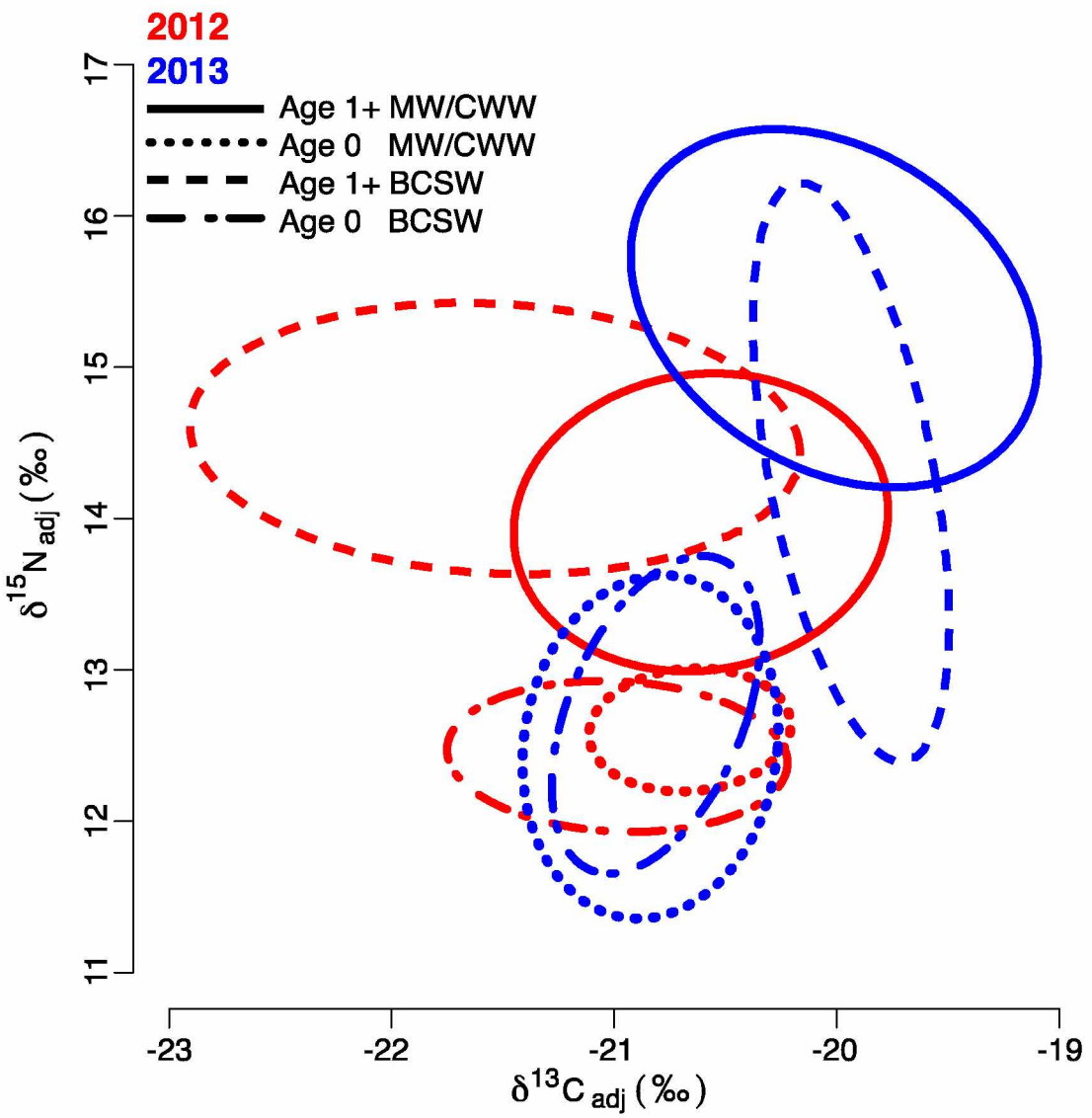

Figure 1.7. Standard ellipse areas representing $\delta^{15}N_{adj}$ and $\delta^{13}C_{adj}$ isotopic niches for age-0 and age-1+ Arctic cod collected during 2012 (red) and 2013 (blue) surface trawl in the Melt Water/Chukchi Winter Water (MW/CWW) and Bering Chukchi Summer Water (BCSW) water masses

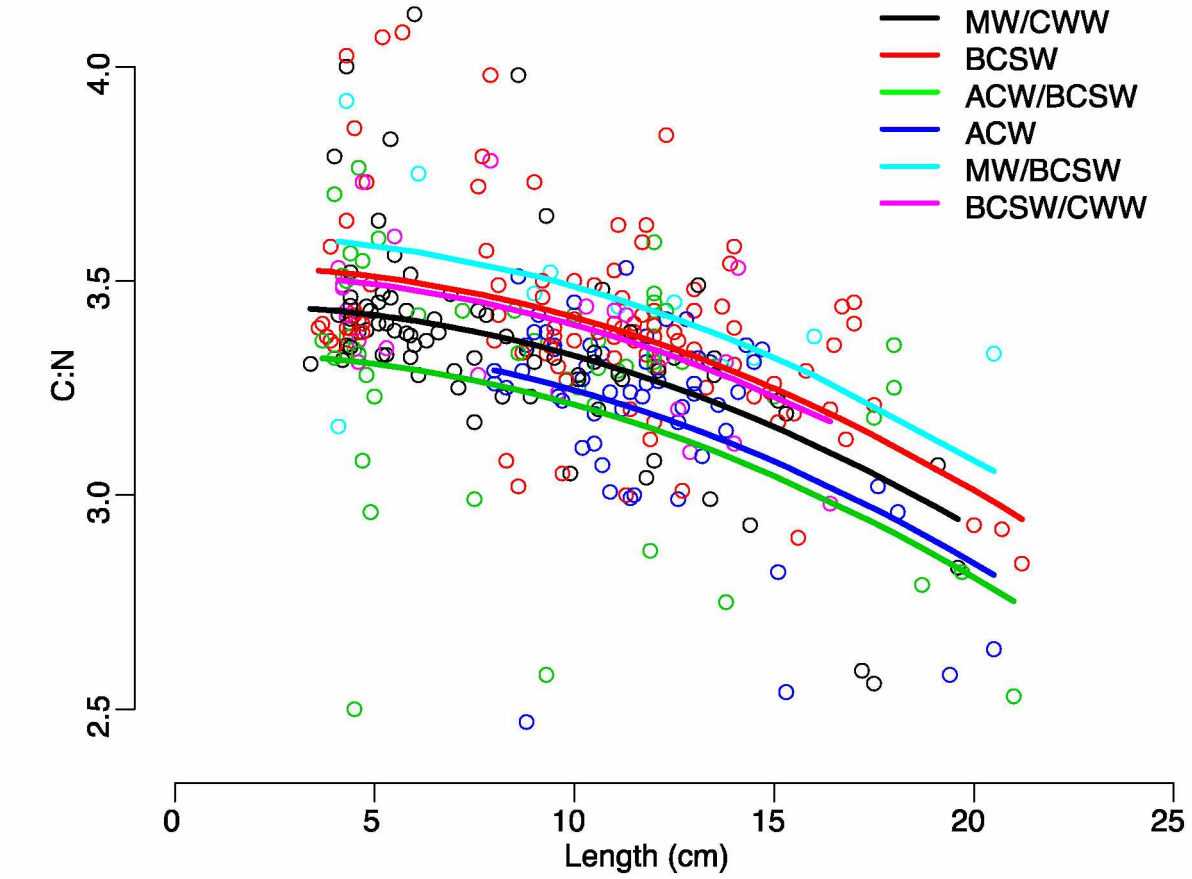

Figure 1.8. Modeled relationships between the C:N and fork length by water mass for 2012 Arctic cod (conditional $r^2 = 0.33$ and marginal $r^2 = 0.58$).

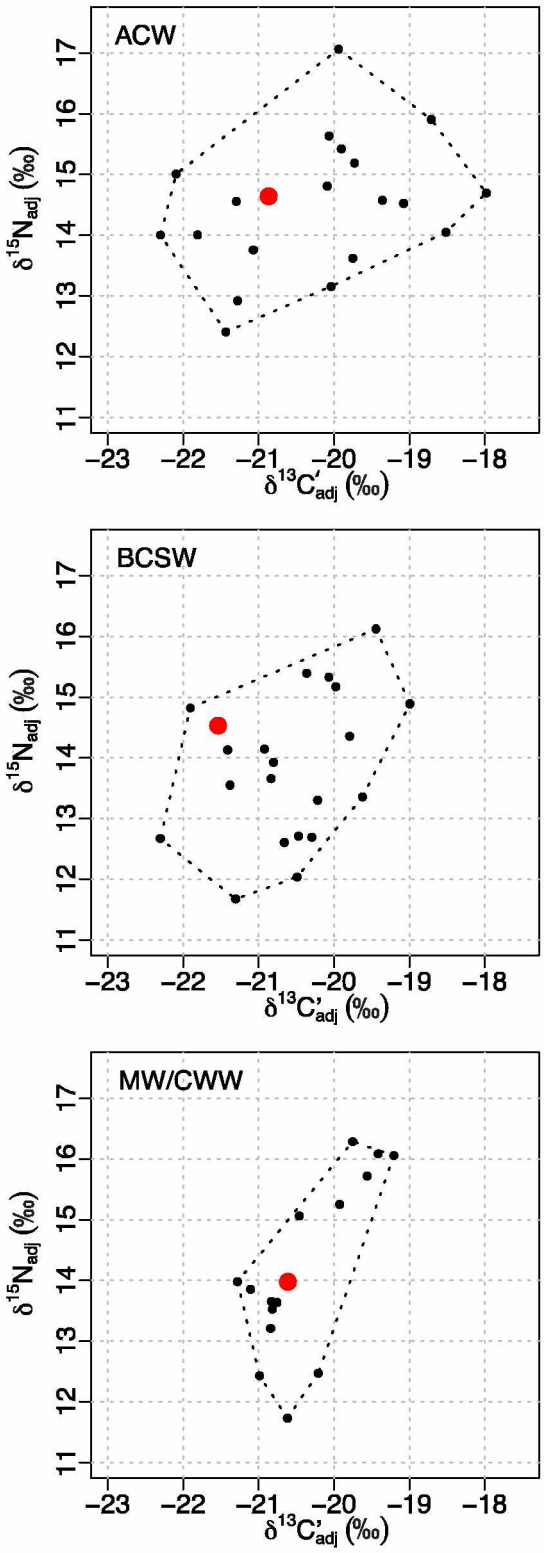

Figure 1.9. Convex hulls encapsulating isotopic niche space ($\delta^{15}N_{adj}$ vs $\delta^{13}C_{adj}$) of fish community by water mass structure in 2012. Each point is a mean value by species and size class (age 1+ and age 0s). The red circles are the mean value for Arctic cod age 1+.

Chapter 2 Environmental and biological influences on the distribution and population dynamics of Arctic cod (*Boreogadus saida*) in the US Chukchi Sea[2]

2.1 Abstract

Arctic cod (*Boreogadus saida*) is the most abundant and widespread forage fish in the Chukchi Sea and was identified as a potential target species in the 2009 North Pacific Fishery Management Council Arctic Fisheries Management Plan. Currently, commercial fishing is prohibited in the US Arctic due to insufficient data to assess the sustainability of potential fisheries. To address this need, comprehensive fisheries oceanography surveys took place throughout the US Chukchi Sea during the summers of 2012 and 2013. High densities of age-0 Arctic cod were observed in the northeastern Chukchi Sea, while older Arctic cod (age-1+) were more widely distributed throughout the survey area. Our objectives were to improve understanding of the factors driving variations in the distribution and abundance of Arctic cod and to assess the current status and dynamics of Arctic cod in the Chukchi Sea. We estimated age structure, abundance, biomass, natural mortality, and reproductive potential using data from the recent surveys combined with available estimates of biological parameters from the literature. Results indicate that temperature is an important driver for the distribution of both age-0 and age 1+ Arctic cod with age-0 cod less likely to be present in warmer waters. Estimates of egg production and early survival suggest that the numbers of mature Arctic cod present in the survey area during summer are unlikely to produce the observed high abundances of age-0 Arctic cod in the US Chukchi Sea. This could imply that either mature Arctic cod migrate to the Chukchi Sea to spawn in the winter, that age-0 fish are advected from outside the study area, or that adult Arctic cod abundance is underestimated. Additional systematic surveys and further research are needed to resolve the origins of age-0 Arctic cod, identify nursery areas, and estimate early life survival.

[2]Marsh JM, Mueter FJ, Quinn TQ. Environmental and biological influences on the distribution and population dynamics of Arctic cod (*Boreogadus saida*) in the US Chukchi Sea. For submission to Polar Biology.

2.2 Introduction

Arctic cod (*Boreogadus saida*) are the most abundant and widely distributed forage fish in the Arctic Ocean and surrounding seas (Lowry and Frost 1981; Barber et al. 1997; Gillispie et al. 1997). They are adapted to low light conditions (Jonsson et al. 2014) and cold temperatures (sub-zero) through the production of anti-freeze glycoproteins (Osuga and Feeney 1978). They play a central role in Arctic food webs, linking upper and lower trophic levels and transferring energy between benthic and pelagic realms (Welch et al. 1992). Because of their high abundance and energy density (Harter et al. 2013), they are an important prey resource for many migrating seabirds (Matley et al. 2012) and marine mammals (Laidre and Heide-Jørgensen 2005; Loseto et al. 2009) and are caught as subsistence food for humans (Magdanz et al. 2010) .

Although their commercial potential has been recognized (e.g., NPFMC 2009), there have been only few examples of historical or current fisheries for Arctic cod. In the Barents Sea there is a longstanding pelagic trawl fishery targeting concentrations of Arctic cod in late autumn during southward spawning migrations. The fishery began in the 1950s with participants mainly from Russia and Norway. Catches peaked at over 348,000 metric tons (mt) in 1971 (Gjøsæter 1995) and continued at much reduced levels with 19,600 mt harvested by Russia in 2011 (ICES 2012). Off the coast of Alaska, small amounts (e.g., average 9 lbs. per household in Kivalina) of Arctic cod are caught in subsistence fisheries in the Beaufort and Chukchi seas (Magdanz et al. 2010). Past fisheries have found commercial uses for Arctic cod, but due to their integral role in the ecosystem, there are concerns over commercial removals. Currently, commercial fishing is prohibited in the US Arctic due to insufficient data to assess the sustainability of a potential fishery (NPFMC 2009).

To address this need for additional data, comprehensive fisheries oceanography surveys took place throughout the US Chukchi Sea during the late summers of 2012 and 2013 (Mueter et al. 2017). High densities of age-0 Arctic cod were observed in the northeast Chukchi Sea during both years (De Robertis et al. 2017b), either in the surface mixed layer or throughout the water column. In contrast, older Arctic cod (age-1+) were more widely distributed throughout the Chukchi Sea during bottom trawl surveys conducted in 2012 (Goddard et al. 2014).

The objectives of this study are (1) to improve understanding of the factors driving variations in the distribution and abundance of Arctic cod in the US Chukchi Sea and (2) to assess the current status and dynamics of Arctic cod in the Chukchi Sea. To meet these

objectives, we used these new survey data combined with available estimates of biological parameters (e.g., fecundity, growth and survival) for Arctic cod from other regions. First, we modeled survey catch per unit effort (CPUE) of age-0 and age-1+ Arctic cod relative to physical (temperature, salinity) and biological (productivity, competitors, prey) factors. Second, we compiled and updated life history information on Arctic cod to estimate their age structure, abundance, biomass, and reproductive potential in the Chukchi Sea. Further, we used a Leslie Matrix model (Leslie 1945) with updated life history parameters and recent survey data to simulate and better understand the population dynamics of Arctic cod. Finally, we examined if the mature summer population of Arctic cod in 2012, as estimated by the survey, could produce the high abundance of age-0 Arctic cod observed during the acoustic survey in 2013.

2.3 Methods

2.3.1 Survey and data collection

In August and September of 2012 and 2013, comprehensive fishery oceanography surveys were conducted in the northeastern Bering Sea and eastern Chukchi Sea bounded by the U.S.-Russia Maritime Boundary to the west and by the 10 m isobath along the Alaskan coast to the east. Main trawling stations were spaced every 55.6 km (Fig. 2.1a & 2.1b; 61 stations in 2012 and 39 in 2013) on a standardized grid. At each main station, pelagic fishes and invertebrates were collected with a 400/601 Cantrawl (122 m headrope, 162 to 1.2 cm mesh) from the upper 25 m of the water column. Oceanographic data were gathered with a conductivity, temperature and depth datalogger (CTD) throughout the water column (SBE 9-11 plus or FastCat CTD, Sea-Bird Electronics, Inc, Bellevue, WA), and zooplankton were collected in paired oblique bongo tows (505 μm and 153 μm cod-end mesh) aboard the F/V Bristol Explorer. Acoustic data were gathered while in transit between stations using a split-beam SimRad ES60 echosounder with backscatter at 38 and 120 kHz (De Robertis et al. 2017a). Midwater trawls were deployed opportunistically when acoustic signals were strong using the same 400/601 Cantrawl, as well as a modified Marinovich trawl (2013 only; 2 m headrope, 6.4 to 0.3 cm mesh). In 2012 only, a concurrent bottom trawl survey was conducted aboard the F/V Alaska Knight at 71 stations (Fig. 2a) using two gear types to sample epibenthic fishes and invertebrates. The 83-112 Eastern bottom trawl (EBT; 25.3 m headrope, 34.1 m footrope and 32 mm mesh cod-end liner) was

towed at all 71 stations, while a 3 m plumb-staff beam trawl (PSBT; 4.1 m headrope, 5.1 m footrope and a 4 mm mesh cod-end liner) was deployed at 39 stations. Temperatures were recorded with a Sea-Bird SBE-39 datalogger attached to the head rope of the EBT (details in Goddard et al. 2014). Subsamples of fishes collected during the bottom trawl survey were measured to the nearest cm, while fishes sampled in the surface and midwater trawls were measured to the nearest mm.

2.3.2 Analysis of environmental and biological influences on Arctic cod distribution

2.3.2.1 Data processing

Due to poor net selectivity of the surface trawl (De Robertis et al. 2017a) and because age-0 Arctic cod often occurred below the sampling depth of the surface trawl net (Alex De Robertis, NOAA, Seattle, pers. comm.), we used acoustic estimates to calculate station-specific age-0 Arctic cod densities (#/km^2). We extracted the mean age-0 Arctic cod (<7.5 cm), and capelin (*Mallotus villosus*) density estimates from acoustic transects (De Robertis et al. 2017b) within a 2.5 nautical mile radius of each surface trawl main station in 2012 and 2013 (Fig. 2.1) using ArcGIS version 10.3. To estimate densities of older (age 1+) Arctic cod on the bottom (Fig. 2.2), we adjusted station-specific CPUE (#/km^2) estimates from the bottom trawl survey to exclude age-0 Arctic cod (≤ 7.0 cm) and to account for gear selectivity (see *biomass, abundance and egg production* section). The 7 cm cutoff was selected based on the overall length-frequency distribution of all Arctic cod sampled, in which the two smallest size modes were separated at approximately 7 cm, and on von Bertalanffy growth parameters (Helser et al. 2017).

We examined if physical (temperature, salinity) and biological (phytoplankton concentration, competitors, prey) factors may be driving the distribution of age 0 and age 1+ Arctic cod using a statistical modeling approach. Potential explanatory variables collected during the survey and included in models for age-0 Arctic cod were sea surface temperature (°C), integrated water column chlorophyll *a* (mg/m^2, Danielson et al. 2017) as a proxy for phytoplankton standing crop, *Calanus* spp. densities (#/m^3; Pinchuk and Eisner 2017) as an indicator of available prey (Gray et al. 2016), capelin CPUE as a likely competitor (Hop and Gjoseater 2013, McNicholl et al. 2016), and lion's mane jellyfish (*Cyanea capillata*) CPUE (#/km$^{2;}$ area swept estimates from the surface trawl catch) as a likely predator (Crawford 2016). Potential explanatory variables used to model age 1+ Arctic cod CPUE were bottom temperature

(°C), bottom salinity, integrated water column chlorophyll *a*, and *Calanus* spp. density. For simplicity, we refer to both acoustic density estimates and trawl survey density estimates as CPUE. Prior to model fitting, CPUE estimates were natural log-transformed (hereafter written as log) to achieve approximate normality of model residuals.

2.3.2.2 Statistical analyses

To address objective 1, we examined the effects of environmental and biological variables on Arctic cod using a generalized modeling approach. The abundances of age-0 Arctic cod in the water column and age-1 Arctic cod on the bottom were modeled separately. Age-0 Arctic cod CPUE had a disproportionate amount of zeros and the combined 2012 and 2013 data were modeled using a 2-stage approach. In the first stage, the presence or absence of age-0 cod was modeled as a binomial response using a logistic regression with a logit link. In the second stage, log-transformed abundances (CPUE) at those stations where age-0 cod were present were modeled using a generalized additive model (GAM) with a Gaussian response.

We first fit full models at each stage that included all of the hypothesized explanatory variables, but no interactions. In the first stage, the logit of the probability of age-0 Arctic cod being present in sample *i* (p_i) was modeled as a linear function of the predictor variables as follows:

(1) $$\log\left(\frac{p_i}{1-p_i}\right) = \alpha_t + \beta_1(SST_i) + \beta_2(Chla_i) + \beta_3(Cal_i) + \beta_4(Cape_i) + \beta_5(Lion_i) + \varepsilon_i$$

where α_t is the intercept for year *t*, β_1- β_5 are coefficients (slopes) for sea surface temperature (*SST*), chlorophyll *a* (*Chla*), *Calanus* spp. density (*Cal*), capelin CPUE (*Cape*), and lion's mane jellyfish CPUE (*Lion*), and ε_i is the residual for sample *i*.

To model variability in age-0 Arctic cod CPUE-where-present (log transformed to approximate normality) we used Generalized Additive Models (GAMs) to allow for potential non-linearities in the relationships between CPUE and explanatory variables. The full-model equation was as follows:

(2) $$\log(Bsa_i) = \alpha_t + f_1(SST_i) + f_2(Chla_i) + f_3(Cal_i) + f_4(Cape_i) + f_5(Lion_i) + \varepsilon_i$$

where Bsa_i is the CPUE of age-0 Arctic cod, α_t is the year-specific intercept for year *t*, f_1- f_5 are non-parametric smooth functions for each explanatory variable, and the residuals, ε_i, are assumed to follow a normal distribution with mean 0 and variance σ_ε^2.

To examine variability in age-1+ Arctic cod, which were present at 70 out of 71 bottom trawl stations, we modeled log-transformed CPUE as a function of selected explanatory variables. The full model equation was as follows:

(3) $\log(Bsa_i) = \alpha_t + f_1(BT_i) + f_2(Sal_i) + f_3(Chla_i) + f_4(Cal_i) + \varepsilon_i$

where α_t is an intercept for each year *t*, f_1-f_4 are separate smoothing functions for bottom temperature (*BT*), bottom salinity (*Sal*), chlorophyll a (*Chla*), and *Calamus* spp. CPUE (*Cal*), and the residuals, ε_i are assumed to follow a normal distribution with mean 0 and variance σ_ε^2.

To identify which environmental or biological variables are most likely to influence Arctic cod presence and abundance, we compared each of the full models to reduced models using a step-wise selection (removing the term with the highest p-value) and selected the best-fit model using Akaike's Information Criterion (AIC; Akaike, 1974). When the difference in AIC values was < 2, the more parsimonious model (fewer parameters) was selected (Burnham and Anderson 2002). Results from the best-fit models were plotted to visualize the estimated relationships between biological or environmental factors and Arctic cod presence or CPUE. The explanatory variables *Chla* and *Cal* were only available for 57 of the 71 stations, so only these stations were used in the initial fitting. If these variables were not present in the best-fit models for the reduced dataset, the model was re-fit using the complete dataset. All regression analyses were performed in the statistical program R (version 3.1.2; R Core Team 2014), and GAMs were fit using the R package mgcv (Wood and Augustin 2002).

2.3.3 Abundance, biomass and egg production estimates

2.3.3.1 Gear Selectivity

To account for known under-sampling of smaller sized fish in the EBT hauls, we used CPUE estimates from the paired PSBT and EBT hauls to estimate gear selectivity for Arctic cod at different lengths. The PSBT has smaller meshes and is effective for sampling juvenile and small adult fishes (e.g., Abookire and Rose 2005), while the EBT has relatively large meshes, which retain larger fishes, but allows for some escapement of smaller fishes (e.g., Somerton et al. 2011). Paired trawls with both the EBT and the PSBT gear types were conducted at 39 of the 71 bottom trawl stations. Paired trawls were typically deployed on the same day, but at four stations the two gear types were used 30-35 days apart. These stations were not included in the selectivity analysis. An additional paired trawl was excluded, in which three Arctic cod were caught in the

EBT but no associated lengths were recorded. Using area-swept (tow distance x net width), we estimated CPUE (#/km^2) within 1 cm size bins for each station and gear type. First, station and gear-specific length frequency distributions were constructed for all Arctic cod captured in a haul or for random subsamples (maximum of 300) of the catch. Length-frequencies from subsamples were extrapolated to the entire haul, and CPUE was calculated by length bin for each gear type and station combination. Arctic cod length-binned CPUEs from the 34 paired hauls were averaged across hauls for each gear type. To estimate selectivity of the two gear types, we made the following assumptions: (1) the selectivity of each gear can be described by a logistic curve, (2) selectivity of the PSBT is close to 1 for small fishes and decreases with length, and (3) selectivity of the EBT increases with length and approaches 1 for large fishes. Selectivity of gear type j in length bin L (y_{jl}) was modeled using the following logistic equation:

(4) $y_{jL} = \frac{1}{1+e^{b_j(x_L - a_j)}}$

where x_L is the mid-point of length bin L, parameter a_j corresponds to size at 50% selectivity for gear type j (PSBT or EBT) and b_j corresponds to the slope of the curve for gear type j. For the PSBT the slope was constrained to be positive ($b \geq 0$), corresponding to decreasing selectivity with length, while for the EBT we assumed $b \leq 0$. We estimated the parameters using a least-squares approach that minimized a weighted sum of squared differences between the predicted length-binned CPUEs for the two gear types. The squared differences for each length bin were weighted by the inverse of the total number of fish in a given length bin. To reduce variability in the weights across length bins and avoid problems with zeros in some length bins, the number of fish per length bin was smoothed using a running average over three consecutive length bins prior to weighting.

2.3.3.2 Abundance

We used the area-swept method to estimate Arctic cod overall abundance and abundance by length across the survey region. One haul with recorded Arctic cod, but no associated length data, was excluded from analysis. It was assumed that the measured sub-sample from each haul was representative of the length frequency of the entire sample. We calculated the selectivity adjusted EBT CPUE (#/km^2) by length bin for each haul, by dividing EBT CPUE estimates by selectivity-at-length ($y_{L,EBT}$). The sampling design was on a standardized grid, with each station representing an area equal to 3091 km^2, except stations close to land, which were assumed to be

representative of all waters within a grid cell that were deeper than 5 m (based on ETOPO1 Global Relief Model; Amante and Eakins 2009). Those stations represented areas ranging from 1024 km^2 to 3069 km^2. We estimated total abundance at length (N_L) across the survey area using the following equation:

(5) $N_L = \sum_{S=1}^{70} CPUE_{L,S}/y_{L,EBT} \times Area_S$

where $CPUE_{L,S}$ is the CPUE of Arctic cod in length bin L at station S. The total abundance of age 1+ Arctic cod was then estimated by summing abundances across all length bins ≥ 8 cm, assuming that smaller Arctic cod were age-0.

2.3.3.3 Biomass

To estimate the biomass of Arctic cod in the eastern Chukchi Sea at the time of the survey, lengths were converted to weights using the length-weight relationship from Helser et al. (2017):

(6) $W = 1.30E^{-5} \times L^{2.9}$

where W is the weight of fish in g and L is length in mm. Selectivity-adjusted abundance estimates from each length bin (≥ 8 cm) were multiplied by the corresponding weight and summed to calculate the Arctic cod age 1+ biomass. The survey area biomass was converted to metric tons (mt). We compared this new biomass estimate with the estimate in the Arctic FMP (NPFMC 2009).

2.3.3.4 Egg production

We calculated potential egg production by Arctic cod sampled in the Chukchi Sea survey area based on the abundance-at-length estimates and maturity and fecundity estimates at length. No data on Arctic cod maturity or fecundity at length are available from the Pacific Arctic region, so we used literature values from Atlantic and Arctic domains around Svalbard (Nahrgang et al. 2014). Assuming that Arctic cod in the Chukchi Sea have a 1:1 sex ratio and spawn every year after reaching maturity (Sakurai et al. 1998), we estimated egg production (E) using the following equation:

(7) $E_D = \sum_{L=8}^{25} \frac{N_L m_{LD} f_{LD}}{2}$

where N_L is the abundance-at-length L (8 – 25 cm), m_{LD} is the proportion of females that are mature-at-length L based on estimates from domain D (Arctic or Atlantic) and f_{LD} is fecundity-at-length L for domain D.

2.3.3.5 Uncertainty

To evaluate uncertainty in selectivity parameters, abundance-at-length estimates, biomass and egg production we used a bootstrap approach. First, the length-binned CPUE values from 34 paired trawls were resampled with replacement by haul to obtain a new bootstrap sample of size 34. The selectivity parameters for the EBT (a and b in Eq. 1) were estimated from this bootstrap sample using the methods described in the gear selectivity section above and the resulting selectivity vector was saved. Next, the length-binned CPUE estimates for the remaining 36 unpaired EBT trawls were resampled with replacement by haul. Finally, using the saved selectivity vector and the combined bootstrap sample of 70 (34+36) CPUE at length vectors, we estimated selectivity-adjusted abundance at length, biomass and egg production as for the original sample. This procedure was repeated 10,000 times to obtain approximate 95% confidence intervals and standard errors for abundance at length, biomass and egg production. Basic bootstrap confidence intervals were constructed based on percentiles of the bootstrap distribution of each quantity of interest (Davison and Hinkley 1997). Finally, a bias correction was applied if the bootstrap means showed a consistent bias with respect to the survey estimates. The bias was estimated as the difference between the bootstrap mean and the survey estimate and then subtracted from the survey mean and from the lower and upper confidence bounds.

2.3.4 Estimates of natural mortality

Natural mortality (M) is a key parameter in population dynamics models and we used three alternative approaches for estimating mortality. First, we assumed a longevity-dependent constant natural mortality (Hoenig 1983) with maximum age set at 8 years (Gillispie et al. 1997):

(8) $\log(M) = 1.46 - 1.01\log(t_{max})$

where t_{max} is the maximum age. Second, we used catch curve analysis to estimate a constant mortality (Quinn and Deriso 1999). For this method, we assumed that the estimated age distributions from the 2012 bottom trawl survey represent the stable age distribution of the population.

(9) $N_a = N_0 e^{-Ma}$

$\log(N_a) = \log(N_0) - Ma$

where N_a is abundance-at-age a. We converted estimated abundance-at-length (N_L) to abundance-at-age (N_a) for age 1+ Arctic cod in the survey area using the selectivity adjusted abundance-at-length data from the EBT and von Bertalanffy growth parameters (Helser et al. 2017). Arctic cod exhibited different growth dynamics north (L_∞ = 197, k = 0.324, t_0 =-1.065) and south (L_∞ = 221, k = 0.297, t_0 =-0.895) of 68.3°N with fish in the north growing at a faster rate, while achieving a smaller asymptotic size (Helser et al. 2017). Because of these regional differences, we estimated the abundance-at-age for each region separately from the selectivity adjusted abundance-at-length data for hauls in each region. Ages were estimated using cohort slicing, which deterministically predicts age from length using the inverse of the von Bertalanffy growth curve (e.g., Ailloud et al. 2014). For this calculation we used the age_slicing function in the R package ALKr (Loff et al. 2014). The minimum and maximum ages were constrained to 0 and 6. Arctic cod have a maximum observed age of 8, but fish older than 5 are rarely observed. Finally, we estimated weight-varying mortality (M_w) for marine fishes (Lorenzen 1996):

(10) $M_w = 3.69W^{-0.305}$

where W is the mean weight at age (Table 2).

2.3.5 Leslie matrix model

We evaluated the estimates of natural mortality (M) in the context of a simple population model, which requires estimates of fecundity-at-age (f_a), survival-at-age (S_a), and abundance-at-age. The Leslie matrix model is an age-structured population model that can be used to simulate population growth or estimate life-history parameters under the assumption that the growth rate and age-structure are stable (Quinn and Deriso 1999). It does not account for density-dependence. For a population with three age groups, the model has the form:

$$(11)\quad \begin{bmatrix} N_{1,\,t+1} \\ N_{2,\,t+1} \\ N_{3^+,\,t+1} \end{bmatrix} = \begin{bmatrix} S_0 f_1 & S_0 f_2 & S_0 f_{3^+} \\ S_1 & 0 & 0 \\ 0 & S_2 & S_{3^+} \end{bmatrix} \begin{bmatrix} N_{1,\,t} \\ N_{2,\,t} \\ N_{3^+,t} \end{bmatrix}$$

where $N_{a,t}$ is the number of females at age a at time t, S is the fraction surviving from age a to age a+1, and f_a is the net fecundity at age a (see below). Using the estimated abundances at age (ages 1 through 6+), three different scenarios for survival and two fecundity scenarios, we

simulated population trajectories over 50 years and calculated the population rate of increase to determine which values of M may result in a stable population.

Survival (S_a) at age a (1+) was calculated as follows (Quinn and Deriso 1999):

(12) $S_a = e^{-M_a}$

where M_a is natural mortality at age a. Survival was calculated for each of the three natural mortality methods described in the previous section.

We estimated two separate fecundity-at-age vectors based on maturity and fecundity at length values from the Arctic and Atlantic domains D, respectively, to bracket likely values for the Chukchi Sea, whose temperatures overlap with the temperature ranges of both domains (Nahrgang et al. 2014). Fecundity-at-age (f_{aD}) was calculated for each age class a (1 through 6+) using the following equation:

(13) $f_{aD} = \frac{\sum N_{aLR} f_{LD} m_{LD}}{N_a}$

where N_{aLR} is the abundance at age a, in length class L and in region R (North and South; see Table 2 for age length key by region), m_{LD} is the proportion of females that are mature at length L based on estimates from domain D (Arctic or Atlantic), f_{LD} is gross fecundity (number of eggs produced per mature female) at length L for domain D, N_a is the abundance estimate at age a (1 through 6+; equation 9), and the summation is over all length classes.

For our final Leslie matrix model input, we estimated survival from spawning to age-1 (S_0) using the equation:

(14) $S_0 = \frac{N_1'}{E}$

where N_1' is the abundance estimate of age-1 cod from the bottom trawl survey and E is the estimated total egg production (eq. 7).

2.3.6 Maximum sustainable yield

We updated estimates of reference points maximum sustainable yield (MSY), fishing mortality rate at MSY (F_{MSY}), and biomass at MSY (B_{MSY}) for Arctic cod in the Chukchi Sea. Values were estimated using equations provided in the Arctic FMP dynamic pool model (NPFMC 2009) and updated life history parameters for natural mortality (M) and age at 50% maturity (m_{50}) and biomass from this study.

2.3.7 Reconciling age-0 and age 1+ abundances

There is an apparent discrepancy between the estimated age-1+ abundances from the bottom trawl survey and the densities of age-0 Arctic cod in the Chukchi Sea estimated from the acoustic survey. While the latter were very high (comparable to age-0 walleye pollock (*Gadus chalcogrammus*) densities in the southeastern Bering Sea; De Robertis et al. 2017b), adult Arctic cod abundances over the shelf were very low. Hence, we explored whether the adult fish that were present in the study area at the time of sampling could have produced the observed number of age-0 fish in late summer. We predicted a range of abundances of late summer age-0 Arctic cod based on the potential egg production of survey estimated Arctic cod, early life history survival, and egg and larval stage durations. The predicted range of abundances was compared to abundance estimates of age-0 Arctic cod from the 2013 acoustic survey (De Robertis et al. 2017b).

In order to predict the expected number of age-0 fish in late summer, we made assumptions about four aspects of early life history: spawning time, hatch timing, egg mortality, and larval mortality. In general, early life survival of Arctic cod is poorly understood and very little is known about the life history of Arctic cod in the Chukchi Sea, so we used values from the literature and borrowed parameters from other north Pacific gadids. The predicted abundance of age-0 Arctic cod (N_0) at the time of the survey (mean sampling date) was estimated using the following equation:

(15) $N_0 = (E \times e^{-M_E t_E}) \times e^{-M_l t_l}$,

where E is egg production (see *egg production* section for calculation, equation 7), M_E is egg daily instantaneous mortality rate, t_E is time to hatch (egg stage duration) in days, M_l is larval daily instantaneous mortality rate, and t_l is time spent as larvae (hatch time to mean sampling date).

First we estimated the numbers at hatch (N_h):

(16) $N_h = E \times e^{-M_E t_E}$.

For egg production (E) we used Arctic domain values for maturity and fecundity to estimate mean egg production (see *egg production* section for calculation, equation 7). Field-based egg mortality rates were unavailable for Arctic cod, so we used laboratory-based values of hatch success (S_E),

(17) $S_E = e^{-M_E t_{E,50\%}}$

which is the fraction of eggs that survived to hatch (N_h/E) and days to 50% hatch ($t_{E,50\%}$), to estimate egg mortality for Arctic cod (Laurel et al. in review) as

(18) $M_E = -\log(S_E)/t_{E,50\%}$

We used a laboratory-based mortality for Arctic cod eggs reared at 0 °C of 0.0021 day^{-1}, viewed as a lower limit of egg mortality, as there is no predation or emigration. As a possibly more realistic alternative, we also used field-based literature values for walleye pollock, which have pelagic eggs that are similar in size and lipid content. We used an average egg mortality estimated over several years for walleye pollock in Shelikof Strait, which was 0.21 day^{-1} (Brodeur et al. 1996). Additionally, egg stage duration values were obtained from the literature. In sub-zero temperatures, Arctic cod eggs tend to hatch between 61 and 85 days after spawning (Altukhov 1981; Sakurai et al. 1998; Laurel et al. in review). For a mean egg duration (t_E) we used an estimate of 72.8 days.

The predicted abundance of age-0 Arctic cod (N_0) at the time of the survey (mean sampling date) was estimated from the estimated numbers hatching (Eq. 16) as:

(19) $N_0 = N_h e^{-M_l t_l}$

To estimate the larval daily instantaneous mortality rate (M_l), we used the raw catch-at-age data from Bouchard et al. (2017), who sampled Arctic cod larvae in the Canadian Beaufort Sea during 2004 and 2008. Ages were divided into 4-day length bins and we tested for differences in the decline of catch with age (slope) using an ANCOVA with an interaction term between year and age, which was not significant. Therefore, the data were combined to estimate a single value for natural mortality of 0.0413 day^{-1}. The mean larval duration (t_l) was estimated based on the size distribution of observed age-0 Arctic cod at the time of sampling (De Robertis et al. 2017b), which were converted to larval durations using a regression of larval duration on length based on data from Bouchard and Fortier (2011; Fig. 2.3).

2.3.7.1 Estimating uncertainty

Uncertainty in the number of eggs at the time of hatching (N_h) and at the time of sampling (N_0) was estimated based on literature-derived or field-based estimates for egg duration, egg and larval mortality, and larval growth, as well as the observed size distribution of age-0 Arctic cod at the time of sampling. Assuming multiplicative errors, the estimated variance for N_h on the log scale, $\log(N_h)$,

(20) $\log(N_h) = \log(E) - M_E t_E$

is given by:

(21) $\mathrm{var}(\log(N_h)) = \mathrm{var}(\log(E)) + \mathrm{var}(M_E t_E)$

We estimated the variance of log(*E*) using the bootstrapped values (see *Uncertainty* section in *Abundance, biomass and egg production estimates*). We further assumed that estimates of M_E and t_E are independent, hence:

(22) $\mathrm{var}(M_E t_E) = \mu_{t_E}^2 \sigma_{M_E}^2 + \mu_{M_E}^2 \sigma_{t_E}^2 - \sigma_{M_E}^2 \sigma_{t_E}^2$

where ${\sigma_{M_E}}^2$ is the estimated variance of egg mortality, μ_{t_E} is the mean egg duration, μ_{M_E} is the mean egg mortality, and ${\sigma_{t_E}}^2$ is the estimated variance of egg duration. We assumed a normal distribution for egg duration, and estimated the variance based on egg duration (time to 50% hatch) for Arctic cod eggs held at temperatures < 0 °C.

(23) ${\hat{\sigma}_{t_E}}^2 = \frac{1}{n-1}\sum\left(t_{E,i} - \bar{t}_E\right)^2$

The variance of egg mortality was estimated using published literature values for walleye pollock (Brodeur et al. 1996) and using sample values from laboratory studies (Laurel et al. in review). Both were assumed to have a normal distribution.

The estimated variance of log(N_0) was estimated as for N_h using:

(24) $\mathrm{var}(\log(N_0)) = \mathrm{var}(\log(N_h)) + \mathrm{var}(M_l t_l)$

where log(N_h) is from equation 18. Assuming that estimates of larval mortality and duration are independent, we get:

(25) $\mathrm{var}(M_l t_l) = \mu_{t_l}^2 \sigma_{M_l}^2 + \mu_{M_l}^2 \sigma_{t_l}^2 - \sigma_{M_l}^2 \sigma_{t_l}^2$

where ${\sigma_{M_l}}^2$ is the estimated variance of larval mortality, μ_{t_l} is the mean larval duration from hatch to August 23rd (mean sampling date), μ_{M_l} is the mean larval mortality, and ${\sigma_{t_l}}^2$ is the estimated variance of larval duration, calculated as:

(26) ${\sigma_{t_l}}^2 = \mathrm{var}\left(\hat{t}_{l,i}\right) + \mathrm{var}(\varepsilon_l)$

which separates variability in larval duration associated with the estimated variance in the observed size distribution at the time of the survey with uncertainty in the regression that is used to predict larval duration from size (Fig. 2.3). Hence, $\mathrm{var}\left(\hat{t}_{l,i}\right)$ is the variance in the predicted larval durations, which is calculated from the length distribution of age-0 fish observed in the 2013 acoustic survey based on the regression in Figure 2.3. The other term captures uncertainty in the predicted values, where $\mathrm{var}(\varepsilon_l)$ is the residual variance from the regression. Uncertainty in

the slope and intercept was small and was ignored for simplicity. To estimate that variance of instantaneous larval mortality we used the standard error of the slope from the combined linear regression model of the catch at age data (Bouchard et al. 2016).

2.4 Results

2.4.1 Environmental and biological influences on Arctic cod distribution

Warm surface temperatures of the Alaska Coastal Current extended much farther north in the study region in 2012 than in 2013 (Fig. 2.1). In 2012, warmer bottom temperatures and lower bottom salinities also extended along the coast to Barrow Canyon, similar to surface conditions (Fig. 2.2). Age-0 fish were largely confined to the northern Chukchi Sea (Fig. 2.1a, b), while age-1+ fish were caught in the bottom trawl throughout the study area (Fig. 2.2a).

The best-fit model for probability of occurrence of age-0 Arctic cod included terms for year, sea-surface temperature, the abundance of capelin, and the abundance of *Calanus* copepods, but only the sea surface temperature term was highly significant (Table 2.1a). Probability of occurrence decreased from close to 100% at the lowest temperatures to less than 20% and 40% at the highest observed temperatures in 2012 and 2013, respectively (Fig. 2.1 c, d), when all other variables were held constant at their means. Probability of occurrence slightly increased with capelin abundance and decreased with *Calanus* abundance (not shown), though the effects were less pronounced.

Based on the best fit model for CPUE-where-present of age-0 Arctic cod, their abundance was significantly related to SST and chlorophyll *a* and differed significantly between 2012 and 2013 (Table 2.1b). CPUE was significantly higher in 2013 compared with 2012 (Fig. 2.1e, f). CPUE was lower at the coldest temperatures, increased to a maximum at ~ 6.5 °C in both years and then decreased sharply at higher temperatures (Fig. 2.1e, f). CPUE was fairly constant at log(*Chla*) values <4 and then decreased with higher values. However, it should be noted that the relationship was marginally significant (p-value = 0.03) and there were only 3 observations of log(*Chla*) > 4: one in 2012 and two in 2013; hence the apparent effect of *Chla* is weak at best.

The best model of age-1 CPUE, based on 57 stations with complete data for all potential explanatory variables, included only bottom salinity as an independent variable, while integrated *Chla*, and zooplankton collected during the surface trawl were not significant (Table 2.1c).

Therefore, we re-fit the model using the full dataset from the bottom trawl survey (71 stations; Table 2.1d). While the best-fit model included both bottom temperature and bottom salinity (Table 2.1d), these variables were strongly confounded (Spearman rank correlation = -0.93, $p<0.0001$) and their effects were difficult to separate. Therefore, we chose to also examine the effects of bottom temperature and salinity on CPUE separately (Fig. 2.2b, d). While age 1+ Arctic cod occurred at all temperatures, CPUE was relatively high at low temperatures, increased to a peak around 6 °C, and declined sharply at higher temperatures (Fig. 2.2b). CPUE increased near linearly with increasing salinities to a maximum at 31 psu (Fig. 2.2d). The lowest abundances of age-1+ Arctic cod occurred in low-salinity, warm Alaska Coastal Water. Because salinity and temperature are highly correlated, it is difficult to separate their relative effects on the distribution of age-1+ Arctic cod, although temperature resulted in a much better fit (ΔAIC = 14.3) and was estimated to have a higher R^2 than salinity when fit independently (Table 2.1d).

2.4.2 Abundance, biomass and egg production estimates

The selectivity of the EBT was reasonably well estimated under the assumption that it follows a logistic curve (Fig. 2.4). Size at 50% selectivity (*a* in Eq. 4) was estimated to be 97.7 mm (95% confidence interval: 74.2 mm – 108.0 mm) and the estimated slope (b) was -0.07 (-0.16 – -0.05). For the PSBT model, the corresponding parameter estimates were a = 125.7 mm (95% confidence interval: 117.0 mm – 148.1 mm) and b = 0.09 (95% confidence interval: 0.06 – 0.93).

The estimated selectivity-adjusted total abundance of age 1+ Arctic cod was approximately 3.9 billion (95% confidence interval: 2.1 – 6.2 billion) with an estimated total adult biomass within the 207,975 km^2 survey area of approximately 44,500 mt (95% confidence interval: 26,583 – 66,970 mt). The reproductive potential of this population was estimated to be 5.9 trillion eggs (95% confidence interval: 3.7 – 8.9 trillion eggs) and 5.8 trillion eggs (95% confidence interval: 3.6 – 8.7 trillion eggs), assuming that maturity is similar to that in the Arctic or Atlantic domains around Svalbard (Nahrgang et al. 2014), respectively.

2.4.3 Estimates of natural mortality

Natural mortality estimates varied substantially between methods and only the larger values resulted in realistic population growth rates in Leslie matrix model simulations. The natural mortality estimate based on longevity (Hoenig) was the lowest at 0.53, catch-curve

analysis resulted in an estimated mortality of 1.40 (SE 0.22, p-value 0.008), and values for weight-varying mortality (Lorenzen) ranged from 1.07 to 1.94 for ages 1 to 6 (Table 2.2). Using estimated mortalities, fecundity values from the Arctic Domain and abundance-at-age estimates (Table 2) as inputs into Leslie Matrix models, we simulated population trajectories. The population growth rate for longevity-based (Hoenig) *M* after 50 years was 102%, for catch curve *M* it was 25%, and for weight varying (Lorenzen) *M* it was 2% (Fig. 2.5). Using the fecundity values estimated from the Atlantic domain, the population growth rates were 5% to 17% higher with the largest difference being for weight-varying M and the smallest difference for longevity-based *M*. Assuming fecundity and maturity values similar to those estimated for Arctic cod in the Atlantic, simulations with the higher natural mortality rates resulted in a more stable population and, therefore, may be more representative of Arctic cod mortality rates in the Chukchi Sea.

2.4.4 Maximum sustainable yield

The larger biomass observed in this study resulted in larger MSY and B_{MSY} values than previously estimated (Table 2.3). It should be noted that the survey area in this study was over twice the size of that covered by the 1990 survey (used to estimate biological reference points in the Arctic FMP). The estimated fishing mortality rate at MSY was highest when the new, very high estimate of natural mortality was used, resulting in an MSY that was about 2/3 of the total estimated biomass (Table 2.3). When natural mortality was held constant fishing mortality rates decreased at the updated lower value of m_{50} = 2.2 years compared to 3.5 years used in the Arctic FMP (Table 2.3); however, the magnitude of the effect was small compared to the effect of natural mortality. Maximum sustainable yield was highest when updated life history parameters M (higher mortality) and m_{50} (earlier maturation) were used (Table 2.3).

2.4.5 Reconciling age-0 and age 1+ abundances

Using our best estimates for egg production, egg duration, egg mortality (2 scenarios), larval duration and larval mortality, we estimated abundances of age-0 Arctic cod at roughly 11 billion fish [95% confidence interval of 750 million - 158 billion (low egg mortality)] and 3 thousand fish [95% confidence interval of 1 - 16 million (high egg mortality)] (Table 2.4). The upper end of the confidence interval assuming low egg mortality was well below the 247 billion age-0 fish estimated from the 2013 acoustic survey (Fig. 2.6), while the point estimates are one

to several orders of magnitude smaller. These results suggest that there are not enough eggs to produce the estimated number of age-0 fish from the acoustic surveys.

2.5 Discussion

The Arctic Eis surveys provided the first comprehensive assessment of the abundance and distribution of Arctic cod throughout the US portion of the Chukchi Sea, showing that adults are demersal throughout the region and broadly distributed on the shelf over a wide range of temperatures but at relatively low abundances. In contrast, young-of-year fish were concentrated at very high densities in the NE Chukchi Sea primarily in the winter water. The observed number of adults in the survey region is unlikely to account for the number of observed offspring, suggesting a missing biomass of adults, advection of young fish from outside the study region, failure of model assumptions, or data quality issues. In addition, we provided the first estimates of natural mortality, which appear to be very high compared to other gadids.

2.5.1 Environmental and biological influences on Arctic cod distribution

Temperature was strongly linked to the distribution of age-0 Arctic cod, which were more frequently encountered in the northern half of the survey area, where temperatures were cooler. In 2013, the cooler winter waters and melt waters were more widespread, as the warmer Alaska Coastal Water (ACW) did not extend north of 70 °N (Danielson et al. 2017) and Arctic cod occupied a larger area and were approximately 3 times as abundant as in 2012 (De Robertis et al. 2017b). The larger extent of the warmer ACW in 2012 may indicate restricted availability of suitable habitat for juvenile Arctic cod, which appear to prefer cooler waters, or may reflect lower levels of spawning, limited advection into the region, or reduced egg and larval survival in 2012. Annual transport was lower through Bering Strait in 2012 (~0.7 Sv) compared to 2013 (~1.1 Sv) (Woodgate et al. 2015), which may imply that fewer eggs and larvae were advected to the Northeast Chukchi Sea from potential spawning sites in the Bering Strait region (C. Vestfals, University of Alaska Fairbanks, pers. comm.). Where age-0 Arctic cod were present, CPUE increased non-linearly with temperature to a peak near 7 °C, coinciding with the temperature of maximum growth rate of laboratory-reared juvenile Arctic cod (Laurel et al. 2016). Similarly, a maximum growth rate at 5.2 °C was observed in the laboratory for early stage larvae and 6.7 °C for later stage larvae (Koenker et al. in press). In contrast, in the Barents Sea the majority of age-

0 Arctic cod occur between 2.0–5.5 °C (Eriksen et al. 2015). However, we used near sea surface temperature for our analysis and while age-0 Arctic cod were typically observed in near-surface waters, they often extended from the surface to near the bottom in warmer waters and, therefore, likely experience lower temperatures on average.

Contrary to expectation, age-0 Arctic cod CPUE decreased with the density of *Calanus*, which are major prey for small Arctic cod in the Chukchi Sea (Gray et al. 2016; Marsh et al. 2017), perhaps suggesting a top-down effect on *Calanus*. Schools of Arctic cod have been observed to locally deplete *Calanus* spp. in Allen Bay in the Canadian High Arctic (Hop et al. 1997). Similarly, zooplankton biomass was negatively correlated with biomass of planktivorous fish during August through early October in the Barents Sea, suggesting top-down control (Stige et al. 2014). We observed a similar negative relationship, suggesting that the high densities of age-0 Arctic cod in the water column may be depleting zooplankton locally in the Chukchi Sea.

GAM results suggest that the distribution of age-1+ Arctic cod was also related to temperature and possibly salinity with a decrease in CPUE at the highest temperatures and at lower salinities. Higher temperatures, lower salinities, and lower nutrients are characteristic of the Alaska Coastal Current (ACC), which flows northward in the Chukchi Sea along the coast of Alaska (Danielson et al. 2017). Though age-1+ Arctic cod occurred throughout the survey area, the lowest densities were observed in the warmest and freshest waters of the ACC, with a steep decline in CPUE when temperatures exceeded 6 °C. Similarly, in laboratory studies, growth rate peaked at 6 °C for 2-year old Arctic cod and survival decreased at 8 °C (Kunz et al. 2016). In contrast, saffron cod (*Eleginus gracilis*), a potential competitor, were most abundant in these warmer coastal waters. They are generally considered a coastal species and the growth rate of juvenile saffron cod exceeds that of Arctic cod at temperatures above about 10 °C (Laurel et al. 2016). Similarly, saffron cod adults have a faster growth rate and larger maximum length compared to Arctic cod (Helser et al. 2017). Integrated *Chla* and zooplankton collected during the surface trawl survey were not significantly related to Arctic cod CPUE from the bottom trawl survey, suggesting that age 1+ Arctic cod were not limited by productivity or prey availability in the water column. However, the lack of a relationship may also reflect the temporal mismatch between surface and bottom trawl surveys that were conducted from two different research vessels.

2.5.2 Biomass, natural mortality and reproductive potential

Given the levels of uncertainty and corrections for survey area, our estimates of biomass are not substantially different from past biomass estimates of Arctic cod in the US Chukchi Sea. Using data from a 1990 survey of the northeast US Chukchi Sea (Barber et al. 1997), which covered a more limited survey area of 98,803 km^2, an Arctic cod biomass of 27,122 mt was estimated for the US Chukchi Sea and used in the Arctic FMP (NPFMC 2009). If we assume that the 1990 biomass distribution was consistent throughout our larger survey area of 207,975 km^2, the total biomass estimate would expand to 57,090 mt, which is well within the 95% confidence intervals of our estimate of 44,500 mt (26,583 – 66,970 mt). In this study, we adjusted for gear selectivity but excluded age-0 Arctic cod ($\leq$ 7 cm) because they are largely pelagic and not efficiently sampled by the large-mesh bottom trawl. Goddard et al. (2014) estimated an unadjusted area-weighted biomass of 31,536 mt (S.E. 210,914 mt) using the 2012 survey data. It should be noted that there was interannual variability in catches between the eight stations that were repeatedly sampled in both 1990 and 1991. The average density of Arctic cod in 1991 was only 22% of the 1990 value for these stations (NPFMC 2009). Similarly, large temporal fluctuations in biomass estimates for Arctic cod have been observed in the Russian Chukchi Sea (Datsky 2015). Biomass estimates have ranged from 12,600 mt in 2008 up to 674,200 mt in 2003, with the most recent estimate being 45,700 mt in 2010 (Datsky 2015). While this at least in part reflects large sampling uncertainty, there is a potential for considerable temporal variability in both the Russian and US portions of the Chukchi Sea, which highlights the need for repeated systematic surveys to assess changes in biomass of Arctic cod and other species of interest.

Only the highest estimated natural mortalities were consistent with a stable population given our assumptions about fecundity, maturity, and age composition. Weight-varying natural mortality estimates (Lorenzen 1996) predicted an annual survival of 14% at 8.2 g for age-1 fish, increasing to 34% at 58.2 g for age-6+ fish, while natural mortality estimates based on catch-curve analysis predicted 25% annual survival. In contrast, natural mortality estimates used in the Arctic FMP predicted an annual survival of 63% based on an average of three natural mortality equations using longevity (maximum age of 7; Hoenig 1983) and mean maturation age (equations 8 and 7; Jensen 1996). The relatively high values of mortality and low survival estimated from our catch-curve analysis and body weight are plausible given Arctic cod's

ecological role as the major prey for many seabirds and marine mammals (Welch 1992; Whitehouse et al. 2014) and potentially high rates of post-spawning mortality (Hop et al. 1995).

Using updated survey data and mortality estimates, we estimated a 765% higher MSY for Arctic cod than the Arctic FMP (NPFMC 2009). However, based on a relatively low biomass, high ecological importance and remoteness of the region, the potential for a viable Arctic cod fishery in the Chukchi Sea is low. Adult Arctic cod were distributed throughout the survey area with a biomass of roughly 44,500 mt and an average station specific CPUE of 0.2 mt/km^2 and 17,500 fish/km^2. In contrast, a much larger biomass of Arctic cod in the Barents Sea (0.1-1.9 million mt, ICES 2012) has supported a commercial fishery targeting cod migrating to their spawning grounds. The low biomass in the Chukchi Sea, combined with a short open water season (limited accessibility), low market value (if sold as fishmeal), remote location, and lack of infrastructure likely make a fishery cost prohibitive. Furthermore, Arctic cod are of high ecological importance, comprising up to 75% of the energy transfer from lower trophic levels to piscivorous seabirds and mammals in Arctic marine food webs (Welch et al. 1992). Specifically, using a mass balance model for the US portion of the Chukchi Sea, Whitehouse et al. (2014) estimated that marine mammals and seabirds consumed 111,830 mt of Arctic cod per year, a value much higher than their estimates from 1990s survey data (Barber et al. 1994). This value is also more than twice as high as the updated age-1+ Arctic cod biomass estimate and about 180% of the estimated annual production (62,300 mt) from this study, which may indicate an under-sampling of Arctic cod by the bottom trawl surveys or a migration of Arctic cod into the area during other seasons. In Whitehouse et al. (2014), the annual production was estimated by multiplying estimated biomass by the annual production to biomass ratio, which is approximately equal to the instantaneous mortality rate under steady state conditions (Allen 1971). Hewitt and Hoenig's (2005) method to estimate mortality based on longevity was used by Whitehouse et al. (2014) and likely resulted in an underestimate of mortality (0.55 year^{-1}), as the current study indicates, and in turn Arctic cod productivity. Regardless, given its current low biomass and its ecological role as important prey, it is unlikely that Arctic cod will attract commercial interest in the US Chukchi Sea.

Based on relatively low abundances of age-1+ and high abundances of age-0 Arctic cod, De Robertis et al. (2017b) hypothesized that the Northeast Chukchi Sea serves as a nursery area for Arctic cod from a much broader region. To test this hypothesis, we compared the

reproductive potential of the observed population of adult Arctic cod in the survey area to the observed numbers of age-0 Arctic cod. We conclude that it is highly unlikely that mature females in the survey area can produce enough eggs to yield the estimated number of age-0 fish observed during acoustic surveys. This suggests that 1) either mature fish are migrating into the Chukchi to spawn in the winter, 2) age-0 fish originate from a larger spawning population outside the study area with the northeast Chukchi Sea serving as a nursery area, 3) we are underestimating the abundance of mature Arctic cod in the study area, 4) we are underestimating their reproductive potential, or 5) incorrectly estimating their early life survival. Arctic cod have been observed to form dense schools in shallow water (Welch et al. 1993), which could have been missed by surveys limited to deeper areas of the shelf (> 15 m). Some caution also is required in interpreting our results, as we borrowed life history parameters from other regions and even other species for egg mortality. The walleye pollock egg mortality from the literature is to be viewed as an upper limit, as it is likely that the egg mortality rate for Arctic cod is much lower because Arctic cod eggs are slightly larger, have a higher lipid content than those of walleye pollock (Laurel et al. in press), and are usually found beneath the ice, where predation is likely to be low. As our lower limit we used a laboratory-based egg mortality rate (Laurel et al. in press), which excluded mortality and emigration. The true mortality rate is likely between the two values.

We gained new insights into the ecology and population dynamics of Arctic cod in the Pacific Arctic through analyzing new survey data, but many aspects of their biology remain unknown. To understand their basic life history and protect vulnerable life history stages, information on spawning locations, spawn timing, winter distributions, and the distribution of early life history stages is needed. For a reliable stock assessment, region-specific estimates of biomass or abundance, natural mortality, growth, and reproductive rates are needed. In this study we provided estimates of abundance, biomass, age structure (based on growth curves in Helser et al. 2017) and natural mortality based on the 2012 survey data. Given rapidly changing ice conditions in the Pacific Arctic, there is a need for continued surveys and biological sampling to assess changes in Arctic cod and other fish populations in the northern Bering Sea and Chukchi Sea. Additionally, region-specific information on fecundity and maturity would benefit assessments, though this will be challenging as it may require under-ice sampling.

Our results provide a snapshot of the abundance, distribution and dynamics of Arctic cod in the Chukchi Sea at a time of rapid climate change. The future of Arctic cod in our study region is uncertain. The Arctic is warming roughly two times as fast as the rest of the globe, which will likely impact cold-adapted Arctic cod. This warming is evident in a reduction of sea-ice extent and thickness (Stroeve et al. 2014) and an increase in temperatures throughout the Arctic at a rate of roughly 0.5 °C per decade in the Chukchi Sea (Jeffries et al. 2014). Although the consequences of these climate changes for fishes in the Pacific Arctic are poorly understood, sub-arctic gadids such as Pacific cod (*Gadus macrocephalus*) or walleye pollock may expand into the Chukchi Sea (Hollowed et al. 2013). These species have temperature-dependent growth rates that exceed those of Arctic cod above 2 °C (Laurel et al. 2016) and, therefore, may outcompete Arctic cod during the summer months. As the waters continue to warm, suitable habitat for age-0 Arctic cod may be further restricted, but also may result in faster growth (Bouchard and Fortier 2008; Laurel et al. 2015, Koenker et al. in press). The upper thermal limits for heart function are about 3 °C cooler for larval Arctic cod than for adults (Drost et al. 2016) and egg hatch rates decline substantially above 3 °C (Laurel et al. in press), indicating early life stages are more vulnerable to climate warming. Under-ice spawning and egg development may not be affected as long as Chukchi Sea spawning areas continue to be cold and ice-covered in the winter. However, earlier sea-ice melt could result in hatching in open water rather than under ice and faster development of larval stages in warmer waters. Exposure to warmer waters could result in high larval mortalities given their known temperature sensitivity. Given current projections for declining sea ice conditions in the northern Bering Sea and Chukchi Sea (https://www.esrl.noaa.gov/psd/ipcc/ocn/timeseries.html), the habitat for Arctic cod in the Pacific Arctic will continue to undergo large changes in coming decades; hence, there is a need for both monitoring to assess changes in Arctic cod and research to better understand the most vulnerable early life stages.

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Table 2.1. Generalized Additive Model fits for models of age-0 Arctic cod presence/absence (a), CPUE-where-present (b), age 1+ Arctic cod (c) and full data set of age 1+ Arctic cod (d). Model associated degrees of freedom (DF), ΔAIC values, R^2 and number of samples (n) are also listed. Rectangular borders highlight selected best-fit models. Significance of individual terms is indicated at four levels (p-values: *** < 0.001 ≥ ** < 0.01 ≥ * < 0.05 ≥ .< 0.1).

	Model parameters	DF	ΔAIC	R^2	n
a)	Additive models, binomial response: age-0 presence/absence				
	Year + SST*** + Chla + Cal* + Cape + Lion	8.7	0.4	0.30	93
	Year* + SST*** + Cal* + Cape* + Lion	7.1	0.0	0.28	93
	Year* + SST*** + Cal* + Cape*	6.0	0.3	0.27	93
	Year* + SST*** + Cape	5.2	2.9	0.26	93
	Year + SST***	3.0	6.0	0.20	93
	SST***	2.0	7.8	0.18	93
b)	Additive models, response: log(age-0 CPUE-where-present)				
	Year*** + SST** + Chla* + Cal + Cape + Lion	10.6	4.5	0.38	56
	Year*** + SST** + Chla* + Cape + Lion	9.6	3.8	0.40	56
	Year*** + SST*** + Chla* + Lion	8.7	1.9	0.40	56
	Year*** + SST*** + Chla*	7.7	0.0	0.41	56
	Year*** + SST***	5.7	6.4	0.31	56
c)	Additive models, response: log(age-1+ CPUE + 1)				
	BT + Bsal*** + Chla + Cal	6.9	3.7	0.30	57
	BT + Bsal*** + Cal	5.9	2.1	0.31	57
	Bsal*** + Cal	5.4	0.3	0.32	57
	Bsal***	4.4	0.0	0.31	57
d)	Additive models, all stations, response: log(age-1+ CPUE + 1)				
	BT*** + Bsal*	7.7	0.0	0.52	71
	BT***	5	6.3	0.45	71
	Bsal***	4.3	20.6	0.32	71

Table 2.2. Gear selectivity adjusted abundance at age, age-length key for Arctic cod S and N of 68.3 N, mean length (cm) and weight at age, proportion mature at age, gross and net fecundity at age estimated from the Arctic and Atlantic domain maturity schedules (Nahrgang et al. 2014), and instantaneous mortality rates.

		Length range (cm)		Mean Length	Mean Weight	Maturity		Gross Fecundity		Net Fecundity		Instantaneous Mortality Rate		
Age	Abundance	South	North	(cm)	(g)	Arctic	Atlantic	Arctic	Atlantic	Arctic	Atlantic	Longevity	Catch Curve	Weight -based
1	2693669430	8 - 11	8 - 11	10.0	8.2	0.11	0.33	6199	4492	825	1735	0.53	1.40	1.94
2	1080503357	12 - 14	12 - 13	12.4	15.4	0.60	0.53	10560	8093	6539	4308	0.53	1.40	1.60
3	83506461	15 - 16	14 - 15	14.4	23.8	0.84	0.67	13431	12482	11466	9026	0.53	1.40	1.40
4	20841380	17	16	16.1	32.9	0.97	1.00	19335	24381	18755	24381	0.53	1.40	1.27
5	17365241	18	17	17.3	40.2	0.97	1.00	21906	24381	21374	24381	0.53	1.40	1.20
6+	25966429	≥19	≥18	19.7	58.2	1.00	1.00	33441	24381	33441	24381	0.53	1.40	1.07

Table 2.3. Updated estimates of maximum sustainable yield (MSY), fishing mortality rate at MSY (FMSY), and biomass at MSY (BMSY) for Arctic cod in the Chukchi Sea, using equations provided in the Arctic FMP (NPFMC 2009) and updated life history parameters for natural mortality (M) and age of 50% maturity (m_{50}) and biomass from this study and 1990 survey (Barber et al. 1997, NPFMC 2009).

	Year	Biomass (mt)	Area (km^2)	M	m_{50}	F_{MSY}	B_{MSY}	MSY
FMP Biomass	1990	27,122	98,803	0.47	3.50	0.70	5,281	3,674
FMP, updated m50	1990	27,122	98,803	0.47	2.20	0.57	10,632	6,049
FMP, updated M	1990	27,122	98,803	1.40	3.50	2.87	6,298	18,074
FMP, updated life history	1990	27,122	98,803	1.40	2.20	2.58	7,519	19,362
Current study biomass	2012	44,500	207,975	0.47	3.50	0.70	8,665	6,028
Current study, updated m50	2012	44,500	207,975	0.47	2.20	0.57	17,445	9,925
Current study, updated M	2012	44,500	207,975	1.40	3.50	2.87	10,332	29,654
Current study, updated life history	2012	44,500	207,975	1.40	2.20	2.58	12,336	31,767

Table 2.4. Predicted age-0 Arctic cod abundance calculated from Equation 15 and associated parameters: egg production, instantaneous daily egg mortality rate, days spent as an egg (hatch time from spawning), daily larval mortality, and time as a larvae. Age-0 Arctic cod abundance were predicted under 2 separate scenarios which used different instantaneous daily egg mortality rates.

Parameter	Mean	SD	Lower	Upper	Based on
Egg production	5.94×10^{12}	1.33×10^{12}	3.69×10^{12}	8.88×10^{12}	Length distribution, Arctic maturity schedule (Nahrgang et al. 2014 and bootstrapped 95% CI)
Egg stage duration (days)	72.83	6.53	60.04	85.62	Estimates from literature values in < 0 C (Altukhov 1981; Sakurai et al. 1998; Laurel et al. in press)
Egg mortality (day-1) 1 *Arctic cod in lab (no predation)*	0.0020	0.0008	0.0005	0.0036	Estimates from samples of laboratory reared Arctic cod eggs at 0 C (Laurel et al. unpublished)
Egg mortality (days-1) 2 *Walleye pollock Shelikof Strait*	0.209	0.054	0.10	0.31	Estimates from walleye pollock (*Gadus chalcogramma*) in Shelikof Strait (Brodeur et al. 1996)
Larval duration (days)	149.00	31.31	87.63	210.37	95% CI (Lengths from acoustic trawl and length hatch date regression from Bouchard and Fortier 2011)
Larval mortality (day-1)	0.041	0.002	0.037	0.046	Larval *B. saida* Canadian Beaufort (Bouchard et al. 2017)
Abundance of age-0s (1)	10,893,271,605		7.59×10^{8}	1.56×10^{11}	
Abundance of age-0s (2)	3,079		1	1.53×10^{7}	

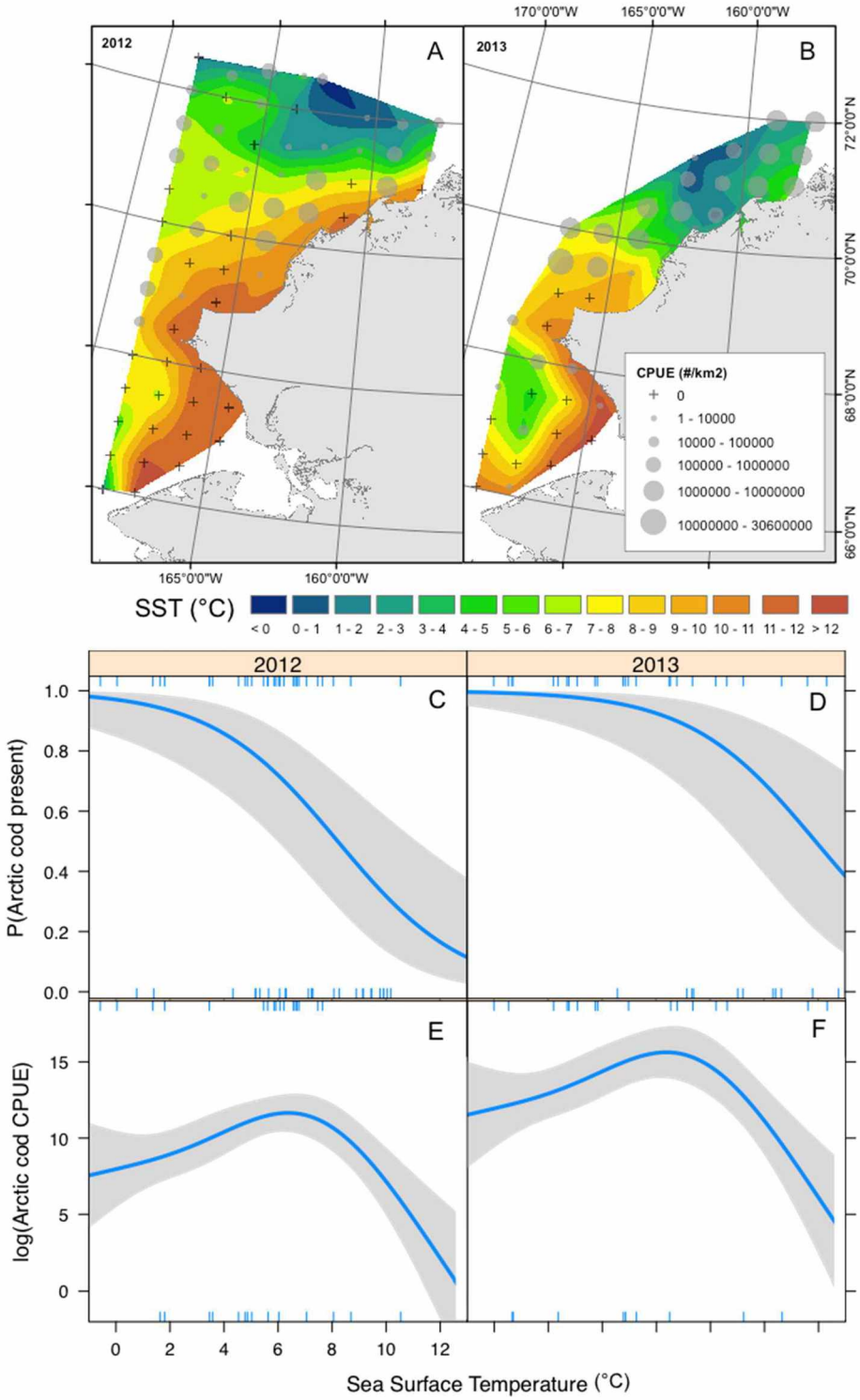

Figure 2.1. Catch-per-unit-effort (CPUE) of age-0 Arctic cod at surface trawl stations (grey circles) and nearest neighbor interpolated sea surface temperature (SST, color contours) in 2012 (A) and 2013 (B), probability of catching age-0 Arctic cod versus SST from best-fit presence/absence model (Table 2.1a) for 2012 (C) and 2013 (D) and model predicted $\log_e$(age-0 CPUE-where–present) versus SST from best-fit model (Table 2.1b) in 2012 (E) and 2013 (F).

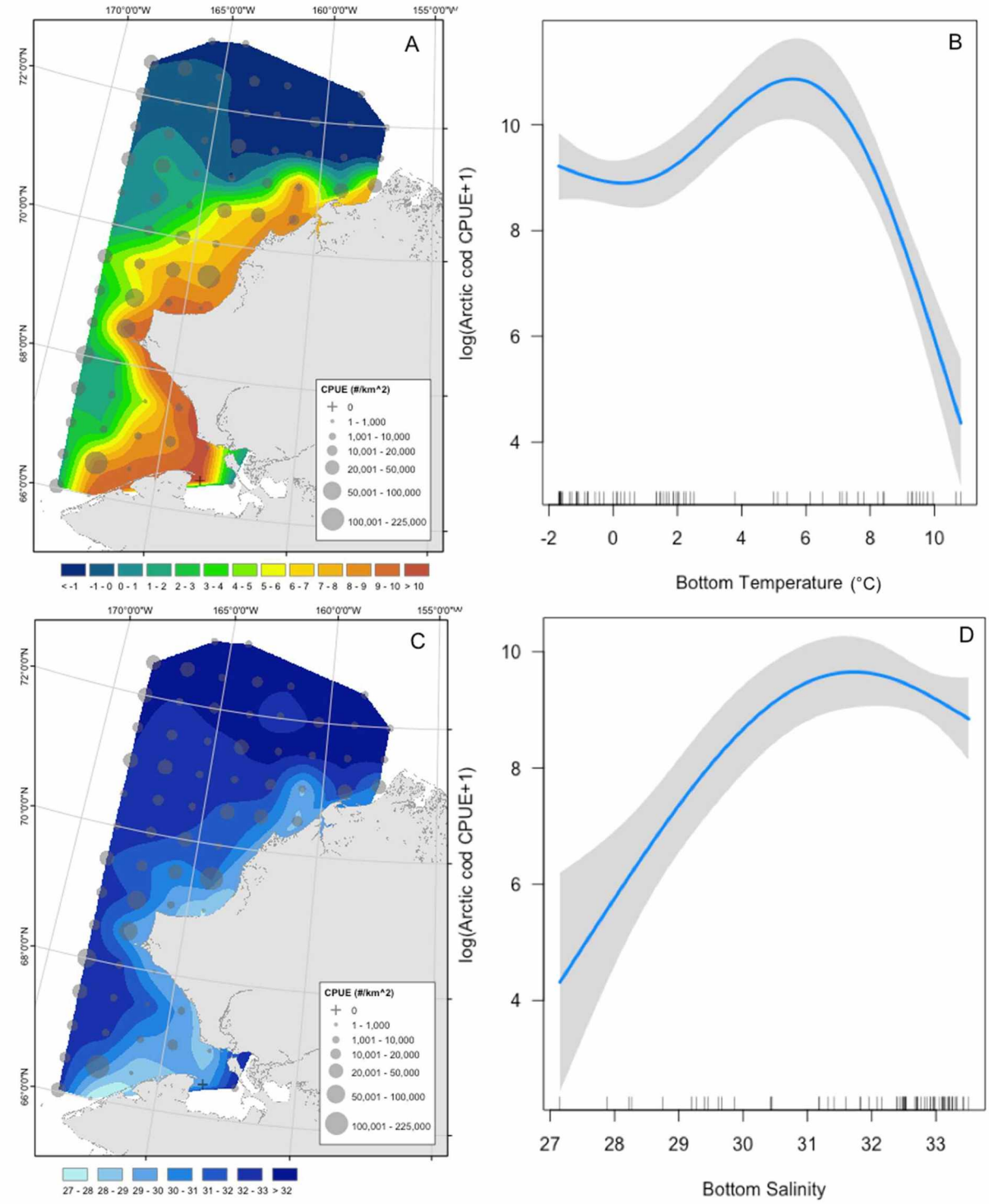

Figure 2.2. Age 1+ Arctic cod CPUE (grey circles) and nearest neighbor interpolated bottom temperature (A) and bottom salinity (C) maps (color contours) in 2012. Model predicted ln(age-1+ CPUE +1) versus bottom temperature (B) and salinity (D). Relationships between CPUE and temperature and salinity were modeled separately.

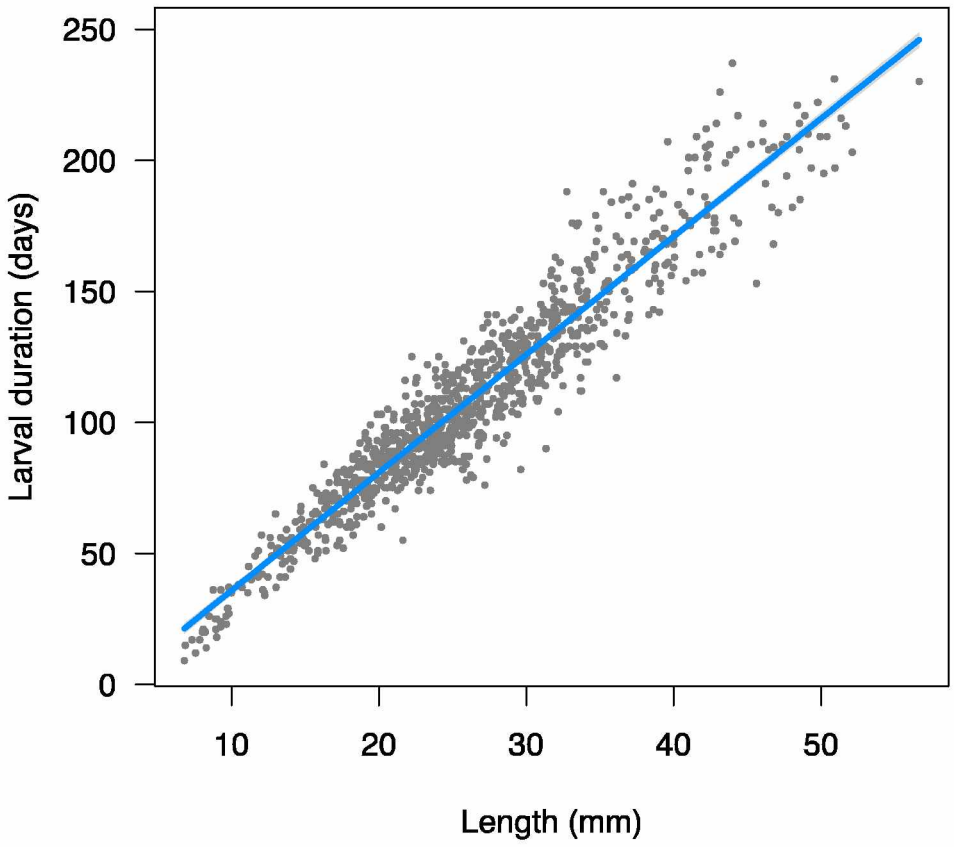

Figure 2.3. Modeled linear regression (blue line) of larval duration (days) on length. Data provided by C. Bouchard (from Bouchard & Fortier 2011).

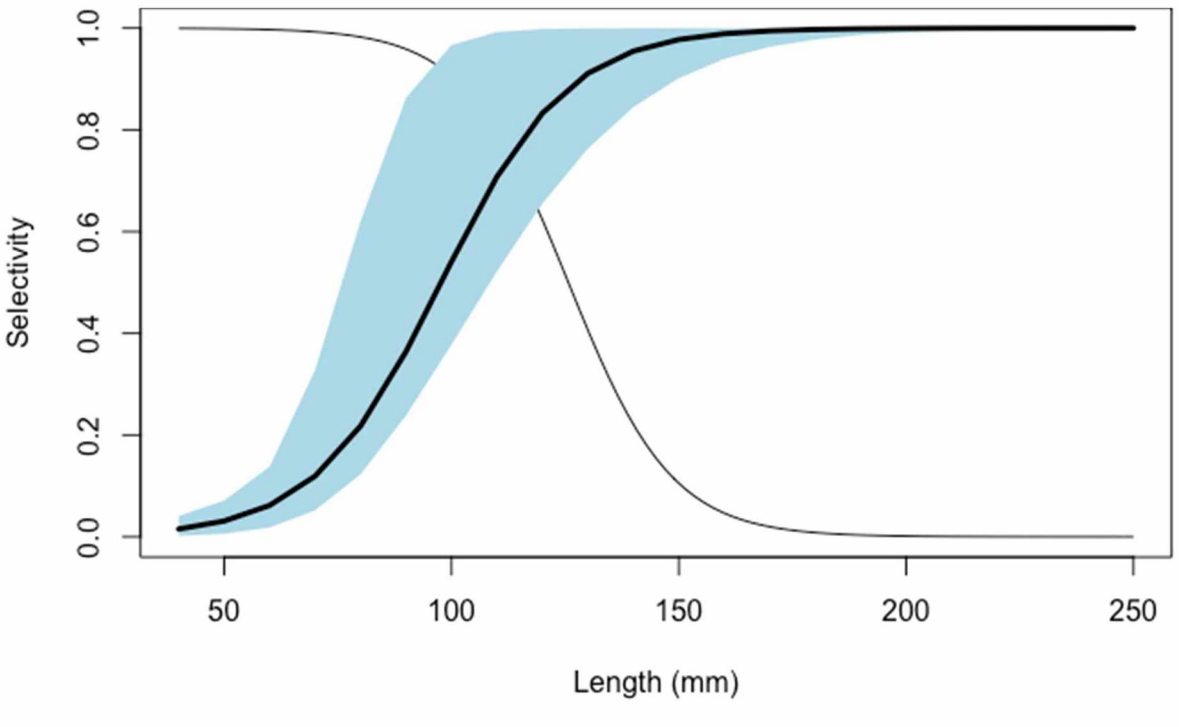

Figure 2.4. Modeled EBT selectivity curve (thick black line) with 95% confidence band based on bootstrapping (shaded polygon) and modeled PSBT selectivity curve (thin black line).

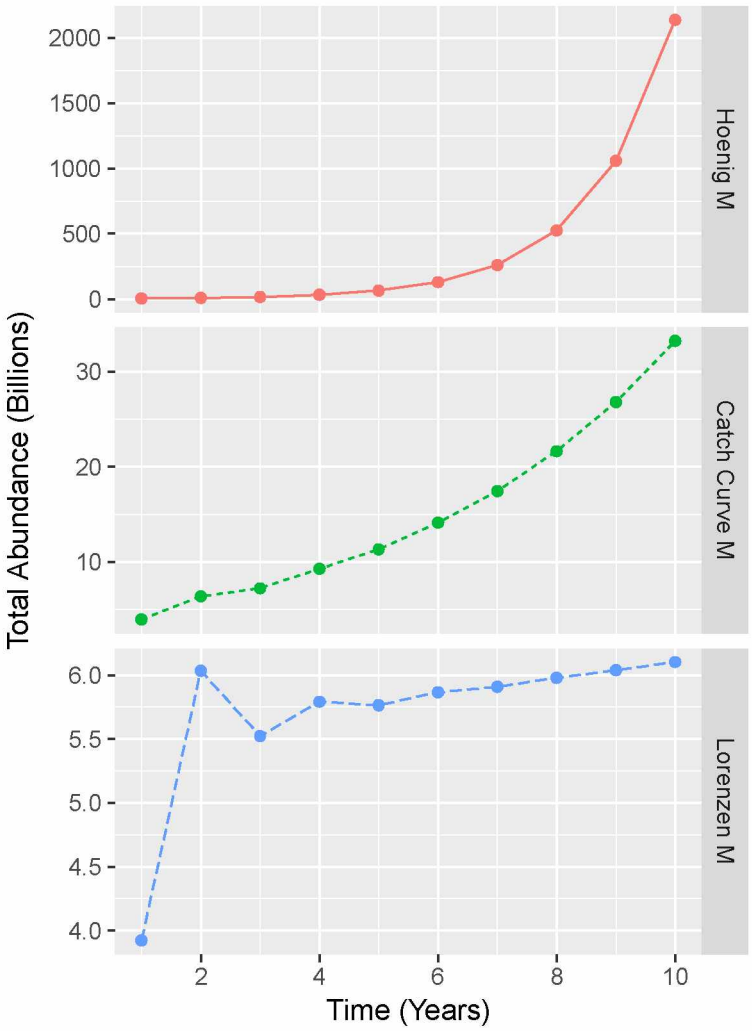

Figure 2.5. Simulated population trajectories from a Leslie Matrix model for three methods of estimating natural mortality over a ten year span: catch-curve (triangles), longevity-based (Hoenig, squares) and weight-varying (Lorenzen, diamonds). Fecundity was estimated using the maturity schedule from the Arctic domain.

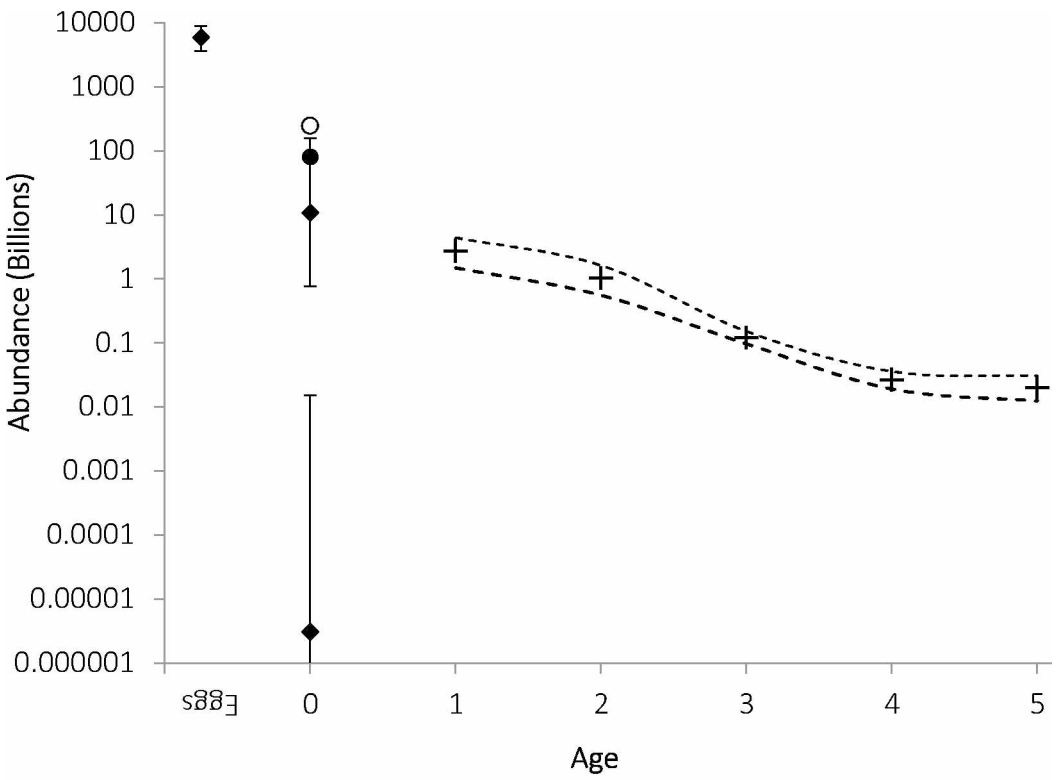

Figure 2.6. Abundance at age for eggs through age 5. Bootstrap bias corrected mean abundances are depicted with crosses for ages 1 through five. Bias corrected bootstrap estimated 95% confidence interval is shown with a dashed line. Age-0 estimates are from the 2012 (closed circle) and 2013 (open circle) acoustic surveys (De Robertis et al. 2017b) and estimated age-0s based on number of eggs and literature values of early life survival based on 2 different scenarios with 95% confidence intervals (diamonds; parameters row 1 in Table 2.4). Estimated egg production (equation 7) with bootstrap estimated 95% confidence intervals is also shown as a diamond.

Chapter 3 Influences of temperature, predators and competitors on Arctic cod (*Boreogadus saida*) at the southern margin of their distribution[3]

3.1 Abstract

Arctic cod (*Boreogadus saida*) is the most abundant and ubiquitous fish species throughout the Arctic Ocean. As such, they serve an important ecosystem role linking upper and lower trophic levels and transferring energy between the benthic and pelagic realms. Our objective is to explore what limits the southern distribution of Arctic cod in Pacific and Atlantic sectors by examining time series of survey and oceanographic data. We quantify the variability in the southern extent of the Arctic cod distribution in the Bering and Labrador Seas, and determine mechanisms (bottom temperature and potential predators and competitors) driving the variability. When temperatures were lower Arctic cod occupied larger areas and had higher abundances in both regions, suggesting that as temperatures increase with climate warming the range of Arctic cod is likely to contract. Temperature had a much larger impact on Arctic cod abundance than competitor abundance (Capelin *Mallotus villosus*, and walleye pollock *Gadus chalcogrammus*) and predator abundance (Pacific cod *Gadus macrocephalus*, Atlantic cod *Gadus morhua* and Greenland halibut *Reinhardtius hippoglossoides*), especially in the eastern Bering Sea. However, when we included data from northern and eastern Bering Sea in 2010 and 2017 Arctic cod were less likely to occur in warmer waters when either Pacific cod or walleye pollock were present. Northward range expansions of subarctic Pacific cod and walleye pollock may further restrict Arctic cod distributions.

[3]Marsh JM, Mueter FJ. Influences of temperature, predators and competitors on Arctic cod (*Boreogadus saida*) at the southern margin of their distribution. For submission to Polar Biology.

3.2 Introduction

Because of extreme seasonality and sub-zero temperatures, there are few fish species that inhabit the Arctic Ocean year round. Arctic cod are the most abundant and ubiquitous fish species throughout the Arctic (Lowry and Frost 1981; Barber et al. 1997; Rand and Logerwell 2011; Geoffroy et al. 2011; De Robertis et al. 2017). They are adapted to low light conditions (Jonsson et al. 2014) and have a high concentration of NaCl (salt) and antifreeze glycoproteins in their blood, which prevents freezing at sub-zero temperatures (Osuga and Feeney 1978). In Arctic food webs, they provide a central role linking plankton to apex predators (Welch et al. 1992). Because of their high abundance and energy density (Harter et al. 2013) they are an important prey resource for many migrating seabirds (Matley et al. 2012) and marine mammals (Laidre and Heide-Jørgensen 2005; Loseto et al. 2009).

The Arctic is warming roughly two times as fast as the rest of the globe with air and sea temperatures expected to rise an additional 5° C and 1.5° C, respectively, by 2100 under moderate carbon emission scenarios (Collins 2013), which will likely impact cold-adapted Arctic cod. This warming is also evident in a reduction of sea-ice extent and thickness (Collins 2013; Stroeve et al. 2014). The consequences of these climate changes for fishes in the Pacific and Atlantic Arctic are poorly understood. In general, adult Arctic cod may be robust to a changing climate, as they can tolerate a large range of temperatures from -1.9°C to 13.5°C, and salinities from 1 to 35 (Craig et al. 1982). However, earlier life stages seem to be more vulnerable to warmer temperatures, as heart function decreases at lower temperatures in larval fish than in adults (Drost et al. 2016) and hatch success declines above 3°C (Laurel et al. in press). Moreover, subarctic gadids such as Pacific cod or walleye pollock may expand northward into the Chukchi Sea (Hollowed et al. 2013). Their juveniles have temperature dependent growth rates that exceed those of juvenile Arctic cod above 2°C (Laurel et al. 2016) and, therefore, these boreal species may outcompete Arctic cod during the summer months. Similarly, demersal species in the Atlantic, most notably Atlantic cod (*Gadus morhua*) have expanded their range northward (Drinkwater 2009, Fossheim et al. 2015). Overall, the fate of Arctic cod in a warming climate is uncertain at the southern edge of their range.

There are four main entry points into the Arctic Ocean: the Bering Strait (between USA and Russia) in the Pacific Arctic, Davis Strait (between Greenland and Canada), Denmark Strait (between Greenland and Iceland) and the Norwegian Sea (between Iceland and Norway). For

this study, we will focus on the Eastern Bering Sea, which is south of the Bering Strait, and the Labrador and Newfoundland Shelf Region south of Davis Strait. The Bering Sea is considered an Arctic inflow shelf as water primarily flows northward towards the Arctic Ocean, while the Labrador and Newfoundland Shelf Region is an outflow region (Carmack and Wassmann 2006). In these regions, at the southern edges of their range, Arctic cod distribution is often limited to the colder water masses (e.g., Wyllie-Echeverria and Wooster 1998). In the Bering Sea there is a persistent cold pool (< 2°C) on the bottom formed in the winter during freeze-up and protected from summer mixing by the thermocline. Between the early 1980s and the mid-2000s, the cold pool retreated approximately 230 km northward (Mueter and Litzow 2008). The cold pool advanced again between 2007 and 2013 to its largest extent in 2012 (Kotwicki and Lauth 2013; Siddon and Zador 2017). In recent years it has retreated again and was virtually absent from the shelf in summer 2018 (R. Lauth, NOAA-AFSC, Seattle, pers. comm.). In the Labrador and Newfoundland Shelf Region, there is a cold intermediate layer (< 0°C) with an approximate thickness of 100-200 m that extends 200-300 km offshore in the summer (Petrie et al. 1988). The area of the cold intermediate layer (CIL) decreases seasonally from spring to fall (November) and is larger following winters with greater ice coverage (Petrie et al. 1988; Prinsenberg et al. 1997). Generally, the area of CIL was anomalously high from the mid-1980s to the 1990s and low from 1995 to 2014 over a time series including years from 1950 to 2017 (Colbourne et al. 2017).

The overall goal of this study is to explore factors that limit the southern distribution of Arctic cod in the Pacific and Atlantic sectors by examining time series of survey and oceanographic data across regions. Specific objectives include:

1. Quantify interannual variability in the southern extent of Arctic cod in the Bering and Labrador seas.
2. Examine and quantify the influence of temperature on variability in the distributions of Arctic cod at their southern margins in the Bering and Labrador seas. We hypothesize that the areal extent of Arctic cod in these seas decreases in years with warmer temperatures.
3. Quantify the relative influence of temperature and competitors or predators on Arctic cod occurrence or CPUE in the Bering and Labrador seas. We hypothesize that both temperature and predator abundances are negatively associated with Arctic cod abundance, but expect temperature to have the largest influence on this cold-adapted species

4. Compare the spatial and temporal dynamics of Arctic cod among different subarctic seas to determine what limits their southern distribution.

Comparing drivers on Arctic cod across multiple systems can strengthen results if similar patterns emerge. In addition, understanding how environmental variability, especially in temperature, and the abundance of potential predators and competitors affect Arctic cod distributions will aid in predicting distributions of Arctic cod under future climate scenarios.

3.3 Methods

3.3.1 Survey Regions and Data

For our analyses, we used biological and oceanographic data from annual groundfish surveys in the eastern Bering Sea (EBS), conducted by the National Marine Fisheries Service (Stauffer 1984), and on the Newfoundland Shelf, Labrador Shelf and the adjacent continental slope (Labrador Newfoundland Region, LNR hereafter), conducted by the Department of Fisheries and Oceans Canada (Hurlbut and Clay 1990). Both survey regions straddle the southern edge of Arctic cod distribution (Fig. 3.1).

3.3.1.1 Eastern Bering Sea

The EBS consists of a broad shallow shelf bounded by Alaska to the east, the Aleutian Islands to the south and dropping to the basin in the west with a shelf break at approximately 180 m depth. Generally, waters from the Pacific flow northward over the shelf, but mean current speeds on the shelf are weak. The middle shelf is typically characterized by cold (< 2°C) bottom waters often referred to as the cold pool. The cold pool is formed during winter ice formation and strong stratification in the summer limits mixing, thereby maintaining the cold pool for much or all of the year. The size of the cold pool each summer depends on the extent of sea ice cover during the preceding winter, as well as the timing of ice retreat during the spring and early summer.

The National Marine Fisheries Service has conducted standardized groundfish surveys on the eastern Bering Sea (EBS) shelf during summer since 1982 (Table 3.1). The survey covers approximately 481,000 km^2 and samples up to 376 stations ranging in depth from 20 to 240 m. Stations are spaced every 37 km on a standardized grid with a higher concentration of stations

(additional stations on grid cell corners) in the waters around St. Matthew Island and the Pribilof Islands. Fishes and invertebrates are sampled with 83-112 eastern otter trawls, which have 25.3 m (83 ft) headropes, 34.1 m (112 ft) footropes and codends with a stretched mesh size of 8.9 cm and 3.2 cm mesh liners. Trawls are towed for approximately 30 min at a speed of 1.54 m/sec. Temperature and depth profiles are recorded using a Sea-Bird SBE-39 datalogger (Sea-Bird Scientific, Bellevue, WA) that is attached to the headrope of the trawl. For additional information on trawl methods and gear, see Conner et al. (2017). During 2010 and 2017, the Bering Sea survey extended into the northern Bering Sea (NBS) encompassing a region in which Arctic cod are more commonly observed. The survey extended north to the Bering Strait and 145 additional gridded stations spaced 37 km apart were sampled in both years.

Biological data on station-specific catch per unit effort (CPUE) in numbers and weight are available for major fish and macro-invertebrate taxa collected by the survey. For this study we used CPUE and presence/absence data for Arctic cod and for potential competitors and predators: walleye pollock CPUE (potential competitor, Whitehouse et al. 2017), capelin CPUE (competitor, Hop and Gjoseater 2013; McNicholl et al. 2016), and Pacific cod CPUE (potential predator – generalist piscivorous predator, Brodeur and Livingston 1988). We also obtained station-specific data on sea surface and bottom temperatures, sampling date, and depth. A number of northern stations were not sampled from 1982 to 1987 and those years were removed prior to analyses (Table 3.1). Confidence of identification for Arctic cod was low in early years (1982 – 1999), and moderate since then, so we used Arctic cod CPUE data only from the latter years (2000-2017) but presence/absence data, which are less sensitive to misidentification, from 1988-2017. Because Arctic cod were rarely caught south of 56.5° N, data south of this latitude were eliminated from analyses.

3.3.1.2 Newfoundland/Labrador Shelf

The LNR survey region includes the eastern Newfoundland shelf (including the Grand Bank) northward to the southern Labrador shelf and the adjacent continental slope to depths up to 1500 m, encompassing North Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, 3O and 3N. The cold (typically -1 to 2° C) Labrador Current flows southward from the Arctic Ocean along the coast of Labrador and Newfoundland to the Grand Banks where it reaches the northward flowing warmer Gulf Stream. The North Atlantic Deep Water is formed by the

cooling of the Gulf Stream when it mixes with the waters of the Labrador Sea (Rhein et al. 2011). The Labrador Current extends along the shelf edge from approximately 50-200 m. This creates a bottom temperature gradient from cooler water to warmer water offshore. Within the LNR, the bathymetry and vertical water structure are more complex than in the EBS. There are several banks and channels throughout the shelves. Along the coast and shelf to roughly 200-300 km offshore, there is a cold intermediate layer of water (<0 □C) created during winter sea ice formation with warmer Atlantic water below (Petrie et al. 1988). The cold intermediate layer impinges on the bottom over shallower portions of the shelf.

The Department of Fisheries and Oceans Canada (DFO) annually conducts a depth-stratified random groundfish survey during fall (typically, Oct. – Dec.), sampling depths from 32 m to 1500 m (Brodie 1996). Fishes and invertebrates are sampled using a Campelen 1800 shrimp trawl with a 29.5 m headrope, 35.6 m footrope, 4.4 cm mesh cod-end and a 1.27 cm mesh liner (McCallum and Walsh 1997). In each Division, a minimum of two 15-min hauls are conducted within each stratum which are determined by area and depth (between 35 and 69 strata per Division), if possible (Brodie 2005). Bottom water temperatures are recorded with a model SBE-19 CTD deployed at all survey stations (Sea-Bird Scientific, Bellevue, WA, USA).

We used biological data on station-specific CPUE in numbers and weight for major taxa collected by the fall groundfish survey from 1995 through 2015 (Tables 3.1 and 3.2). As in the EBS, we used CPUE and presence/absence data for Arctic cod and CPUE for potential competitors and predators: capelin (competitor), Atlantic cod (predator, Lilly 1991; Yaragina and Dolgov 2009; ICES 2012) or Greenland halibut (predator, Bowering and Lilly 1992; ICES 2012). Additionally, we used haul-specific environmental data on bottom temperature, depth, latitude and longitude. Prior to analyses, we eliminated hauls with poor gear performance, which had unreliable catch data. To compare distributions across a consistent survey region over time, we eliminated sampling stations north of 55° N, south of 42.5° N, and east of 47° E. In addition, we eliminated several years with poor survey coverage (Table 3.1).

3.3.2 Data Analysis

3.3.2.1 Interannual variability in spatial extent of Arctic cod

To assess among-year variation in the distribution of Arctic cod, we used binomial generalized additive models (GAMs) to model the presence or absence of Arctic cod as a function of latitude, longitude, year, depth and Julian day for each region. The logit of the probability of Arctic cod being present in haul *i* in year *t* ($p_{i,t}$) was modeled as a linear function of the predictor variables as follows:

(1) $$\log\left(\frac{p_{i,t}}{1-p_{i,t}}\right) = \alpha_t + f_{1,t}\left(Lat_{i,t}, Long_{i,t}\right) + f_2\left(Depth_{i,t}\right) + f_3\left(Day_{i,t}\right)$$

where α_t is the intercept for year *t*, $f_{1,t}$ is a smooth bivariate function of latitude and longitude (*Lat*, *Long*) by year, and f_2- f_3 are smooth univariate functions of Depth (*Depth*), and Julian day (*Day*). The spatial terms (*Lat*, *Long*) were included to account for large-scale spatial trends that could not be attributed to the other covariates and to account for spatial autocorrelation. Julian day (*Day*) was included to account for seasonal trends and differences in sampling dates among years. Thin-plate regression splines were used for all terms. The maximum degrees of freedom (i.e., k-1) for the smoothing functions were constrained to 24 (EBS) and 39 (LNR) for bivariate spatial terms for speed of computation. Models were then used to predict probability of occurrence by year over the survey area in each region. For each year, we then computed the spatial extent of Arctic cod as the fraction of the survey area where probability of occurrence exceeded 20%, hereafter defined as the core habitat area for Arctic cod ('core area'). All regression analyses were performed in the statistical program R (version 3.1.2; R Core Team 2014), and GAMs were fit using the R package mgcv (Wood and Augustin 2002).

3.3.2.2 Influence of temperature on Arctic cod presence

We examined the influence of temperature on the distribution of Arctic cod both within and across years. First, to fill in missing temperature values and for the projections described below, we modeled summer bottom temperatures for each survey region using a GAM as follows:

(2) $$\mathrm{BT}_{i,t} = \alpha_t + f_{1,t}\left(Lat_{i,t}, Long_{i,t}\right) + f_2\left(Depth_{i,t}\right) + f_3\left(Day_{i,t}\right)$$

where $\mathrm{BT}_{i,t}$ is the predicted bottom temperature at station *i* in year *t* and other terms are as described above for modeling probability of occurrence. The model was fit using the available

bottom temperatures (Table 3.1) assuming Gaussian errors. For analysis of interannual variability, we used the intercept α_t as an index of annual mean bottom temperature for each region. The maximum degrees of freedom for the smoothing functions were constrained to 5 for depth and day to avoid over fitting the data and ease of interpretation and to 59 for bivariate spatial terms. To test if there was a relationship between area occupied (see *Interannual variability in spatial extent of Arctic cod)* and mean bottom temperature, we used a linear regression analysis.

To examine the influence of temperature on spatial distributions within years, we estimated the average relationship between probability of occurrence and bottom temperature using a binomial GAM for each region:

(3) $\log\left(\frac{p_{i,t}}{1-p_{i,t}}\right) = \alpha_t + f\left(BT_{i,t}\right)$

A year-specific intercept (α_t) was included to account for differences in the average probability of occurrence among years that are unrelated to temperature, such as fluctuations in overall abundance of Arctic cod. The maximum degrees of freedom was constrained to 3 for *f*. The estimated relationship was examined for a possible "threshold" temperature above which the probability of occurrence of Arctic cod rapidly declines.

3.3.2.3 Arctic cod density (CPUE) as a function of temperature, predators and competitors

To examine the influence of temperature and competitors or predators on Arctic cod in the EBS and LNR we used methods similar to Ressler et al. (2014). First, we used GAMs with a compound Poisson-gamma distribution (Tweedie distribution with an index parameter $1 < p < 2$; Tweedie 1957, Jorgensen 1987) and a log link to model the relationship between Arctic cod CPUE ($\log(Bsa_i)$) as response variable and temperature, latitude and longitude, year, and log-transformed CPUE values of either a predator (Pacific cod, Greenland Halibut or Atlantic cod) or competitor (capelin or walleye pollock) as independent variables. We used the Tweedie distribution to accommodate a high proportion of zeroes in Arctic cod catches (e.g., Shono 2008). The Tweedie distribution has a positive mass at zero, but is otherwise continuous and it includes the Poisson ($p = 1$) and negative binomial ($p=2$) distributions as special cases. We fit the full model and several reduced models (Table 3.2). We also considered using a bivariate smoother with latitude and depth instead of latitude and longitude and compared model fits. Depth is moderately correlated with longitude and most fish species are known to have preferred

depth ranges, hence the model may be biologically more meaningful. However, species distribution models without depth may have greater explanatory power (Pinsky et al. 2013).

Before fitting the models of Arctic cod CPUE, missing bottom temperatures were estimated by fitting the model in equation 2. For each region/competitor or predator combination, a best-fit model was selected from the models in Table 2 using Akaike's Information Criterion (AIC; Akaike, 1974). If there was a difference of <2 in the AIC for the candidate models, the most parsimonious (fewest degrees of freedom) model was selected (Burnham and Anderson 2002). The maximum degrees of freedom for the smoothing functions were constrained to 5 for log(CPUE) and bottom temperature, and 59 for the bivariate smoothers.

To assess the relative importance of temperature versus competitor or predator effects, we used the best-fit model to predict Arctic cod CPUE under five different scenarios: 1) average competitor (or predator) CPUE and temperature across all years at each grid cell, 2) competitor (or predator) CPUEs from the highest abundance year with average temperatures (high competitor/predator scenario), 3) competitor (or predator) CPUEs from the lowest abundance year and average temperatures (low competitor/predator scenario), 4) temperatures from the coldest year with average competitor (or predator) CPUEs (low temperature scenario), and 5) temperatures from the warmest year with average competitor (or predator) CPUEs (high temperature scenario). We computed relative effects as the log of the ratio of predicted Arctic cod CPUE under the high scenarios divided by CPUE under the low scenarios in each grid cell. Predicted Arctic cod values <0.1 were set to 0.1 (smallest observed value) in effects calculations to avoid dividing values by zero, resulting in an undefined effect. A relative effect of zero indicates that there is no change between high and low. A positive value indicates that Arctic cod CPUE increases with an increase in either temperature or competitor or predator and a negative value indicates that CPUE decreases with increasing temperature or competitor values. We also computed the absolute effects to highlight the areas of largest absolute changes in abundance (often areas of higher average abundance). For each grid cell and model output, the standard error and a 95% confidence interval was calculated for the absolute effects in each individual grid cell ($se_{c,g}$) using the following equation:

(4) $$se_{c,g} = \sqrt{se_{h,g}{}^2 + se_{l,g}{}^2}$$

where $se_{h,g}$ and $se_{l,g}$ are the standard errors of predicted log(Arctic cod CPUE) at the high scenario and at the low scenario, respectively. We multiplied $se_{c,g}$ by 1.96 and added and subtracted that

value to the fitted log(absolute effect) to get the 95% confidence interval at each grid. If the 95% CI did not contain zero, the absolute effects were plotted.

For consistency and to more easily compare results between regions, changes in Arctic cod abundance in the LNR were predicted on a regular grid with a spatial resolution matching that in the EBS (approximately 37 x 37 km). Over this grid, we used spatial GAMs to estimate bottom temperature, Atlantic cod CPUE, capelin CPUE and Greenland halibut CPUE by year. These estimates were used to determine the years with high and low average competitor and predator CPUEs and temperature values over the grid cells and to estimate CPUEs and temperatures for each grid cell in each year. The resulting values were used to predict Arctic cod CPUE for the 5 scenarios listed above and to calculate relative and absolute effects as described for the EBS.

3.3.2.4 Northern and Eastern Bering Sea 2010 and 2017

The extension of the standard summer bottom trawl survey into the northern Bering Sea in 2010, a cold year, and 2017, a warm year, provides an opportunity to examine the roles of temperature, competitors and predators on Arctic cod over a broader region. Large changes were observed in the abundance and distribution of a number of species between 2010 and 2017. For example, the abundance of Pacific cod and walleye pollock increased substantially in the northern Bering Sea in 2017, while the abundances of Arctic cod decreased (Siddon and Zador 2017).

We combined data from the northern and eastern Bering Sea (NEBS) for these two years and applied an approach similar to that applied to the standard survey area to examine the influence of competitors, predators and temperature on Arctic cod occurrence over a larger spatial range. First, we fit the data to the same models in eqn 3 and Table 3.2 to assess whether results over a larger area for these two contrasting years are consistent with those of the longer-term but spatially more restricted data set. We further examined the relationship between Arctic cod occurrence, predator or competitor occurrence and bottom temperatures, using binomial GAMs to model the relationship between probability of occurrence of Arctic cod and temperature by year in the presence and absence of walleye pollock, capelin or Pacific cod.

3.4 Results

3.4.1 Interannual variation and influence of temperature

In the EBS, Arctic cod tend to occur within the cold pool, whose extent varies from year to year (Fig. 3.2). But in some years (e.g., 1994 and 1995) the cold pool extends past the area of their distribution and in other years (e.g., 2010 and 2016) the core area extends past the cold pool. In the LNR, the core area similarly varies with the extent of cooler water. However, in the northern part of the LNR the core area often extends beyond the colder waters (<2 °C) into warmer areas, whereas in the south the cooler waters often extend beyond the core area of Arctic cod (e.g., 2012, 2013 and 2015; Fig. 3.3).

In the EBS, the core area of Arctic cod decreased by 9.5% with an increase of 1 °C in mean summer bottom temperature (p-value < 0.001; $R^2 = 0.41$; Fig. 3.4). Mean summer bottom temperatures ranged from 0.56 °C in 2012 up to 4.2 °C in 2016 and the core area ranged from 1% of the total survey area in 1996 to 58% in 2010. In the LNR, we also found a decreasing but non-significant trend between core area and mean fall bottom temperature (slope = -0.15; p-value = 0.11; $R^2 = 0.18$; Fig. 3.4). In the LNR, the mean fall temperatures had a much narrower range from 1.9 °C in 2000 to 2.9 °C in 2011 (overall mean 2.2) than in the EBS. The core area ranged from 28% of the area used in our analysis in 2012 to 65% in 1996 (Figure 3.4).

Averaged across all years, Arctic cod occurred at higher temperatures in the LNR than in the EBS. In both regions, the probability of occurrence was highest at low temperatures but fell below 50% at approximately 2.5 °C in the LNR, while it was below 50% above 0 °C in the EBS (Fig. 3.5).

3.4.2 Influence of temperature, predators and competitors

In the EBS, the best-fit model for estimating Arctic cod CPUE included terms for bottom temperature, log(capelin CPUE), and an interaction between temperature and capelin (Table 3.3). In all cases, including both temperature and a predator or competitor resulted in a better fit than temperature alone (Fig. 3.6). The temperature effects were consistently strong and negative across models, while the interspecific effects were weak (Fig. 3.6). Spatially, temperature had a much larger relative effect on Arctic cod CPUE than potential competitor or predator abundances. Overall, the predicted Arctic cod CPUE increased up to 320-fold in some grid cells

between the warmest and the coldest year (Fig. 3.7). The greatest temperature effects occurred along the eastern edge of the cold pool.

The relative effects of potential competitor and predator abundances were mixed. Arctic cod CPUE increased with capelin CPUE up to a maximum and decreased, but was highly uncertain, at the highest capelin abundances (Fig. 3.6). Spatially, Arctic cod abundance was predicted to be higher over much of the survey region during a year with high capelin abundances (positive effects, Fig. 3.7). In contrast, Arctic cod CPUE decreased significantly with increasing walleye pollock CPUE at intermediate walleye pollock abundances (Fig. 3.6). Spatially, increases in walleye pollock CPUE were associated with decreases in Arctic cod abundance in the most northerly grid cells, which are consistently cold and have larger abundances of Arctic cod, but had an apparent positive effect to the south and east. Arctic cod CPUE decreased significantly and non-linearly with increasing abundances of Pacific cod (Fig. 3.6). Pacific cod had a similar pattern of effects as pollock on Arctic cod CPUE, but with positive relative effects along the southern edge of the area of occurrence. The absolute effects of walleye pollock on Arctic cod CPUE were significant in only 2 grid cells (negative in the northeast), while none of the grid cells had significant Pacific cod effects (Fig. 3.7). Similar to the relative effects, capelin had significant positive effects in the northeast and along the southeastern edge of the cold pool.

In the LNR, the best-fit model for estimating Arctic cod CPUE included covariates for bottom temperature, log(Greenland halibut CPUE) and an interaction between temperature and Greenland halibut (Table 3.3). All terms were significant in the full model ($p < 0.05$). The inclusion of temperature and competitor or predators improved the fit of all models relative to the temperature only model (Table 3.3). The temperature effect was consistent across models with a higher predicted Arctic cod CPUE at temperatures below 2 °C that decreased to a minimum at 4-5 °C, but increased again at higher temperatures (Fig.3.8). The interaction term was not significant in the models that included Capelin as an explanatory variable. In the LNR, the relative effects of temperature, predators and competitors on Arctic cod CPUE had a similar order of magnitude. Increases in temperature on the northern part of the shelf and along much of the shelf break were associated with decreases in Arctic cod abundances (Fig. 3.9). Similar to the EBS, the estimated temperature effects were negative across much of the survey region, but had a smaller magnitude because the temperature differences between the warmest and coldest year

were much smaller. Temperature had a significant negative absolute effect on Arctic cod CPUE at the northernmost stations and along the central part of the shelf in the northern half of the survey region (Fig. 3.9). Increases in Greenland halibut along the shelf break were associated with large relative increases in Arctic cod CPUE, whereas in the nearshore increases in Greenland halibut were associated with moderate decreases in Arctic cod CPUE (Fig. 3.9). Atlantic cod had negative absolute and relative effects over much of the shelf, where their abundances were highest, but were positively associated with Arctic cod in northern offshore areas. In contrast, capelin largely had positive effects on Arctic cod abundance, especially in the north (Fig. 3.9).

3.4.3 Northern and Eastern Bering Sea 2010 and 2017

Combining data from the Northern and Eastern Bering Sea (NEBS) survey regions, the average bottom temperature was 1.7 °C in 2010 and 3.0 °C in 2017. The predicted probability of Arctic cod occurrence decreased with bottom temperature down to 4 °C, increased to a secondary peak at 8 °C and then declined at warmer temperatures (Fig. 3.10). The secondary peak was associated with areas of relatively warm temperatures in the northern Bering Sea that had relatively high abundances of Arctic cod. Arctic cod were not observed at the highest temperatures, which exceeded 13 °C in Norton Sound during the 2017 survey (Fig. 3.11).

Arctic cod CPUE over the expanded survey area in 2010 and 2017 was significantly related to bottom temperature, competitor, and predator abundances (equations from Table 3.2). The best-fit models of Arctic cod CPUE fit with each of the competitors or predators (capelin, walleye pollock and Pacific cod) had similar AIC values and, therefore, fit equally well (Table 3.4). Similar to the EBS, all best-fit models included a strong negative bottom temperature effect that was consistent across models (Fig. 3.12, see also Figs. 3.6, 3.8). The model including Pacific cod in addition to bottom temperature without an interaction term had the lowest AIC and suggested a negative effect of high Pacific cod abundances on Arctic cod CPUE (Table 3.4; Fig. 3.12). The best capelin model, which included an interaction term, suggests a positive association between Arctic cod and capelin in the NEBS on average, though the effect was small, similar to the positive relationship we found using the longer time series for the EBS.

Arctic cod had a higher probability of occurrence over a wider range of temperatures when either Pacific cod or walleye pollock were absent than when they were present (Fig. 3.13a,

b). This difference was larger in 2017 when temperatures were warmer and more Pacific cod and walleye pollock were present in the northern Bering Sea. The presence or absence of capelin had less impact on the occurrence of Arctic cod. There was no evidence of a competitive interaction as Arctic cod were on average more likely to occur when capelin were present at temperatures below 5 °C (Fig. 3.13c).

3.5 Discussion

In this study we investigated potential drivers influencing Arctic cod occurrence and abundance in the Bering Sea and in the Newfoundland and Labrador shelf region. In both areas, Arctic cod occupied larger areas and had higher abundances when temperatures were lower, suggesting that the range of Arctic cod is likely to contract in a warming ocean. Temperature had a much larger impact on Arctic cod abundance than competitor or predator abundance, especially in the EBS. The effects of potential competitor and predators on Arctic cod were mixed and in some cases unexpected. We found little evidence of competitive interactions between Arctic cod and capelin in either region as both of these cold-adapted species appeared to vary similarly in abundance and distribution with temperature fluctuations. In contrast, we found some significant negative relationships between the abundance of another potential competitor in the EBS (walleye pollock) and between known predators (Pacific cod, Atlantic cod, Greenland halibut) and the abundance of Arctic cod. Spatially, these negative effects were most pronounced in areas of the shelf with colder bottom temperatures, where Arctic cod were more abundant. We found additional evidence of potential negative interactions over the larger NEBS region, where the probability of Arctic cod occurrence declined more rapidly with increasing temperature when Pacific cod or walleye pollock were present. Thus, the northward range expansions of an opportunistic subarctic predator such as Pacific cod or potential competitors such as walleye pollock may further restrict the distribution of Arctic cod during warm years.

Of the investigated drivers, temperature appeared to have the largest influence on the distribution and abundance of Arctic cod in both the EBS and LNR and the likelihood of occurrence decreased rapidly with increasing temperatures. Previous studies have found similar links with temperature at the southern margins of Arctic cod's range (Monstad and Gjøsæter 1987; Lilly et al. 1994; Wyllie-Echeverria and Wooster 1998; Rajasakaren 2013; Astthorsson 2016). In the waters northwest of Iceland, Arctic cod were most commonly found in

temperatures between -0.5 °C and 2.5 °C and the probability of occurrence declined with increasing temperatures (Astthorsson 2016). Similarly, in the Barents Sea, Rajasakaren (2013) found that most Arctic cod ages 1-5 were found at temperatures below 0.5 °C and none at temperatures above 4 °C. Similar to our study, Monstad and Gjøsæter (1987) found that Arctic cod in the Barents Sea occupied a larger area when temperatures were colder during the period from 1977 to 1981. While the earlier studies did not examine the effects of competitors or predators on the distribution of Arctic cod, these studies and our results demonstrate that Arctic cod distribution in subarctic waters is closely linked to temperature fluctuations.

However, while Arctic cod primarily occur at temperatures below about 2°C, we found a secondary peak in the probability of occurrence at 8°C when including data from the northern Bering Sea. Similarly, north of Bering Strait in the Chukchi Sea the highest CPUEs of age-1+ Arctic cod occurred at temperatures around 6°C in 2012 (Chapter 2). Furthermore, laboratory studies have found that growth rates of 2-year old Arctic cod peaked at 6°C (Kunz et al. 2016; Laurel et al. 2016), but survival decreased at 8°C (Kunz et al. 2016). These observations suggest that Arctic cod are limited by other factors besides cold temperatures in much of their potential range and may prefer moderate temperatures when no or low abundances of subarctic fishes are present. However, in the presence of subarctic competitors and predators, Arctic cod may be limited to cooler waters where they have a growth advantage over other gadid species (e.g. Laurel et al. 2016).

The effects of potential competitors and predators on Arctic cod at the southern edge of their distribution, were mixed. Unexpectedly, the abundance of capelin, a known competitor (Orlova et al. 2009; McNicholl et al. 2016), was positively associated with Arctic cod abundance in both the LNR and EBS. Additionally, the presence of capelin had no or positive effects on the probability of occurrence of Arctic cod in the NEBS. Like Arctic cod, capelin have a preference for colder water, most commonly found in waters ranging from -1 to 6°C (Rose 2005). In order for competition to exist, species need to co-occur and share a limited resource, such as prey. Competition between capelin and Arctic cod has been observed in the Barents Sea (Orlova et al. 2009) and in the Canadian High Arctic (McNicholl et al. 2018). Arctic cod likely outcompete capelin in the Barents Sea in warmer years (2004-2005) when their range overlaps, as the body condition of capelin was reduced by 40% in areas where Arctic cod were present during those years (Orlova et al. 2009). There was no clear evidence of a negative relationship between

capelin abundance and Arctic cod abundance in the LNR during the autumn of 1978 to 1993 (Lilly et al. 1994), consistent with the current study. These results should be interpreted with caution because capelin, a pelagic forage fish, as well as smaller Arctic cod may not be sampled effectively with large bottom trawls. However, results based on presence/absence data are less sensitive to potential variations in catchability or size selectivity. Overall, we found no evidence that the presence of capelin negatively impacted either Arctic cod abundance or probability of occurrence in the study areas.

In contrast to capelin, we found evidence for negative interactions between walleye pollock and Arctic cod in the Bering Sea based on both abundance and presence/absence data. First, increases in abundance of walleye pollock within the cold pool had negative effects on Arctic cod abundance. Second, the presence of pollock in the NEBS restricted the range of temperatures over which Arctic cod occurred and reduced their probability of occurrence relative to areas where pollock were absent. Together these results suggest a direct and negative effect of walleye pollock on Arctic cod in areas where Arctic cod are abundant. In the EBS, Arctic cod were mostly observed within the cold pool (<2 °C), while age-1 and age-2 walleye pollock mostly avoid the cold pool (Wyllie-Echeverria and Wooster 1998), suggesting that the potential for competition is low due to their spatial separation. Laboratory experiments also show that juvenile walleye pollock prefer temperatures > 2°C, unless they are foraging or avoiding predators (Sogard and Olla 1993). Subdividing the fish species (both walleye pollock and Arctic cod) into age or length classes may help clarify competitive interactions as younger walleye pollock have a different distribution than older and larger pollock (Barbeaux, 2018), and are more likely to compete with Arctic cod for similar prey. Older and larger (> 40 cm) walleye pollock may exhibit shifts in diet to piscivory (Urban 2012) and, therefore, may also prey on Arctic cod. Smaller walleye pollock may outcompete and displace Arctic cod at the intermediate temperatures observed in parts of the northern Bering Sea, or larger pollock may exert predation pressure on Arctic cod.

The generalist predator Pacific cod had mixed effects on Arctic cod abundance in the EBS. Pacific cod is an opportunistic predator and we are not aware of any direct evidence that they are consuming large numbers of Arctic cod. However, our results suggest that the presence of Pacific cod appears to negatively impact Arctic cod in the NEBS, as their probability of occurrence decreased and their temperature range was more restricted when Pacific cod were

present. It should be noted, that another interpretation could be that both Arctic cod and Pacific cod are responding to an environmental cue that is correlated with temperature, instead of the presence of Pacific cod limiting Arctic cod's thermal niche.

The abundance of two potential predators on Arctic cod in the LNR, Atlantic cod and Greenland halibut, were significantly and non-linearly related to Arctic cod abundances, and had mixed effects on Arctic cod across the survey region. Arctic cod have been regularly observed in the diet of both species (Lilly 1991, Bowering and Lilly 1992, ICES 2012), particularly when capelin were absent. As expected, increases in abundance of Atlantic cod had a negative effect on Arctic cod over much of the shelf. However, while Arctic cod abundance was negatively related to the abundance of Greenland halibut when abundances of the latter were low, for example over some shallower portions of the shelf, Greenland halibut were positively associated with Arctic cod over much of the outer shelf and slope where Arctic cod are generally less abundant. Greenland halibut tend to move offshore as they grow, with older individuals inhabiting deeper water, possibly as part of a spawning migration to Davis Strait (Bowering and Brodie 1991), and these larger halibut (>69 cm) appear to be switching from a pelagic fish diet to a predominately groundfish diet (Bowering and Lilly 1992). Bowering and Nedreeas (2000), reported Greenland halibut being the most abundant at depths ranging from 400-1000 m and bottom temperatures between 2°C and 6°C in the Northwest Atlantic. Possibly, Greenland halibut on the outer shelf and slope may be targeting other prey, though the reasons for this apparent positive relationship are unclear.

One potential caveat is that these bottom trawl surveys may be undersampling Arctic cod. In deep water, age 1+ Arctic cod are often found forming schools in the midwater between depths of 100-400 m (Parker-Stetter 2011; Geoffrey et al. 2011). This is unlikely an issue in the relatively shallow Bering Sea where large schools often impinge on the bottom, but problematic in the LNR where depths exceed 400m and the colder water is in the intermediate layer.

I demonstrated that with warming temperatures the area occupied by Arctic cod is likely to decrease resulting in a contraction of the southern range Arctic cod. This is further supported by a study by Alabia et al. (2018), which looked at the distributional responses of species to past climate changes (winter sea ice and winter sea surface temperature) in the EBS. Winter sea ice extent is highly correlated with summer bottom temperatures in the Bering Sea (Wyllie-Echeverria and Wooster 1998). When compared to other species, Arctic cod were especially

sensitive to climatic changes (Alabia et al. 2018), which may be due to early life history and dispersal constraints and suggests that Arctic cod may be a good "bellweather" species for changes at the transition zone between the Subarctic and Arctic. Other studies have documented generally northward shifts in distribution with warming in the Bering Sea across a range of species, but the responses vary across species (Mueter and Litzow 2008; Pinsky et al. 2013; Morley et al. 2018). However, these studies were limited to the standard survey areas in the Southeast Bering Sea and did not explicitly consider species interactions. In this study, we demonstrated that species interactions have a significant impact on the distribution of Arctic cod, especially when including data from the Northern Bering Sea.

Given projected temperature increases, Arctic cod will almost certainly play a much diminished role in the NEBS and LNR in the future, with unknown consequences for the ecosystem and the species that currently depend on Arctic cod for food. In the LNR, the sea surface temperature is predicted to increase by 1.4°C and the bottom temperature by 1.6°C by 2069 (Han et al. 2018). Similarly, temperatures on the EBS shelf are projected to increase 1-2□C by 2040 (Hermann et al. 2016). Our results suggest that these temperature increases will lead to a reduction in Arctic cod in both regions. Recent observations in the Bering Sea suggest that changes are occurring at a more rapid rate than previously expected. For example, sea-surface temperatures in the Bering Sea during 2016 were the warmest on record (Walsh et al. 2018), the Bering Sea had persistently low ice cover in 2017/2018 (NSIDC 2018), the cold pool that usually occupies much of the Bering Sea shelf during summer was completely absent and very few Arctic cod were caught during the 2018 EBS summer groundfish survey (R. Lauth, NOAA-AFSC, Seattle, pers. comm.). The cold pool typically serves as a refuge for Arctic cod and acts as a thermal barrier to demersal subarctic fish, such as walleye pollock and Pacific cod (Sigler et al. 2011). The lack of the cold pool allowed subarctic species to expand northward and very high abundances of both walleye pollock and Pacific cod were observed in the northern Bering Sea during the 2018 survey (R. Lauth, NOAA-AFSC, Seattle, pers. comm.). It appears that a borealization of the northern Bering Sea is occurring and the impact of the combination of warmer temperatures and increases in subarctic gadids on Arctic cod is unfavorable.

While both regions are expected to warm, which will likely negatively impact Arctic cod distribution, the underlying physical oceanography of these two vastly different systems and the associated advection of larvae, nutrients and heat may accelerate or delay the process. The LNR

is an Arctic outflow shelf with cooler Arctic waters flowing southward along the coast that may act as a refuge for Arctic cod and provide a buffer against the effects of warming. In contrast, the Bering Sea is an inflow shelf with warmer Pacific water flowing northward to the Arctic, which may accelerate warming and the response of Arctic cod in the region. To further improve our understanding of the dynamics of Arctic cod, region-specific information on spawning locations, larval dispersal and migratory behavior are needed, along with studies on how those are tied to physical drivers.

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Table 3.1. The total number of successful hauls recorded in groundfish surveys in the Eastern Bering Sea and Newfoundland/Labrador Shelves each year and the number in which Arctic cod are present and bottom temperature (BT °C) data are available. Survey years shaded with dark grey were excluded from analysis. Light grey survey years were excluded from analysis on Arctic cod CPUE in the Eastern Bering Sea.

	Eastern Bering Sea			Newfoundland/Labrador		
Year	Hauls	Presence	BT	Hauls	Presence	BT
1982	334	1	329			
1983	353	5	351			
1984	355	34	346			
1985	357	10	314			
1986	354	46	345			
1987	357	5	354			
1988	373	45	371			
1989	374	5	362			
1990	371	23	308			
1991	372	46	336			
1992	356	48	317			
1993	375	22	333			
1994	375	107	291			
1995	376	49	353	506	281	503
1996	375	3	363	942	451	916
1997	376	21	355	845	357	828
1998	375	39	351	855	298	839
1999	373	58	348	744	314	733
2000	372	34	348	672	214	627
2001	375	27	361	764	274	725
2002	375	8	366	587	229	581
2003	376	14	368	588	172	578
2004	375	28	367	329	142	325
2005	373	22	347	674	223	670
2006	376	64	371	376	111	376
2007	376	87	376	332	78	332
2008	375	101	375	188	97	178
2009	376	46	376	586	224	573
2010	376	153	376	699	258	699
2011	376	48	376	564	113	563
2012	376	115	374	627	130	627
2013	376	61	376	639	197	639
2014	376	12	376	421	178	421
2015	376	34	376	686	289	686
2016	376	70	376			
2017	376	49	376			

Table 3.2. Set of GAMs fit to assess the relationship between the natural log of Arctic cod CPUE in haul *i* (log(Bsa_i)) and year, latitude and longitude, bottom temperature and competitors or predators. The full model includes a tensor product interaction term t_i between temperature and competitors or predators.

Model
Full model
$\log(Bsa_i) = \alpha_t + f_1(Lat_i, Long_i) + f_2(BT_i) + f_3(\log(CPUE_i)) + t_i(\log(CPUE_i), BT_i) + \varepsilon_i$
Full model without interaction term
$\log(Bsa_i) = \alpha_t + f_1(Lat_i, Long_i) + f_2(BT_i) + f_3(\log(CPUE_i)) + \varepsilon_i$
Predator/competitor only
$\log(Bsa_i) = \alpha_t + f_1(Lat_i, Long_i) + f_3(\log(CPUE_i)) + \varepsilon_i$
Bottom temperature only
$\log(Bsa_i) = \alpha_t + f_1(Lat_i, Long_i) + f_2(BT_i) + \varepsilon_i$
Spatial model
$\log(Bsa_i) = \alpha_t + f_1(Lat_i, Long_i) + \varepsilon_i$

Table 3.3. Degrees of Freedom (df), change in Akaike Information Criterion from best-fit model (ΔAIC), and deviance explained for the models listed in Table 3.2 fitted to survey data from the Eastern Bering Sea and Labrador Newfoundland Region. A single asterisk denotes the best-fit model by species and a double asterisks denotes the best-fit model from the region.

Model	df	ΔAIC	Deviance Explained
Eastern Bering Sea			
Walleye pollock			
Full model*	86.0	30.8	86.5
Full model without interaction term	76.8	38.7	86.2
Predator/competitor only	74.7	320.9	83.1
Pacific cod			
Full model	83.5	33.3	86.4
Full model without interaction term*	74.4	29.8	86.2
Predator/competitor only	73.8	285.9	83.5
Capelin			
Full model**	82.0	0.0	86.7
Full model without interaction term	75.5	6.6	86.5
Predator/competitor only	74.3	324.1	83.0
Environmental only			
Bottom temperature only	70.9	53.9	85.9
Spatial model	69.6	383.9	82.2
Labrador Newfoundland Region			
Capelin			
Full model	87.4	151.9	77.5
Full model without interaction term*	80.3	146.2	77.5
Predator/competitor only	77.4	642.8	75.0
Atlantic cod			
Full model*	94.6	96.8	77.9
Full model without interaction term	83.1	208.2	77.2
Predator/competitor only	77.7	748.0	74.5
Greenland halibut			
Full model**	95.1	0.0	78.3
Full model without interaction term	83.9	108.9	77.7
Predator/competitor only	79.5	692.6	74.8
Environmental only			
Bottom temperature only	79.0	223.2	77.1
Spatial model	74.4	771.3	74.3

Table 3.4. Degrees of Freedom (df), change in Akaike Information Criterion from best-fit model (ΔAIC), and deviance explained from the fitted models listed in Table 3.2 fitted to survey data from the North and Eastern Bering Sea in 2010 and 2017. A single asterisk denotes the best-fit model by species and a double asterisks denotes the best-fit model from the region.

Model	df	□AIC	Deviance Explained
North and Eastern Bering Sea (2010 & 2017)			
Walleye pollock			
Full model*	62.2	1.2	81.8
Full model without interaction term	57.6	9.1	81.3
Predator/competitor only	57.5	95.1	78.4
Pacific cod			
Full model	68.0	15.1	81.7
Full model without interaction term**	56.9	0.0	81.5
Predator/competitor only	56.7	70.8	79.2
Capelin			
Full model*	61.0	0.2	81.9
Full model without interaction term	54.9	16.1	81
Predator/competitor only	56.9	107.1	77.9
Environmental only			
Bottom temperature only	51.7	21.8	80.5
Spatial model	51.8	111.7	77.3

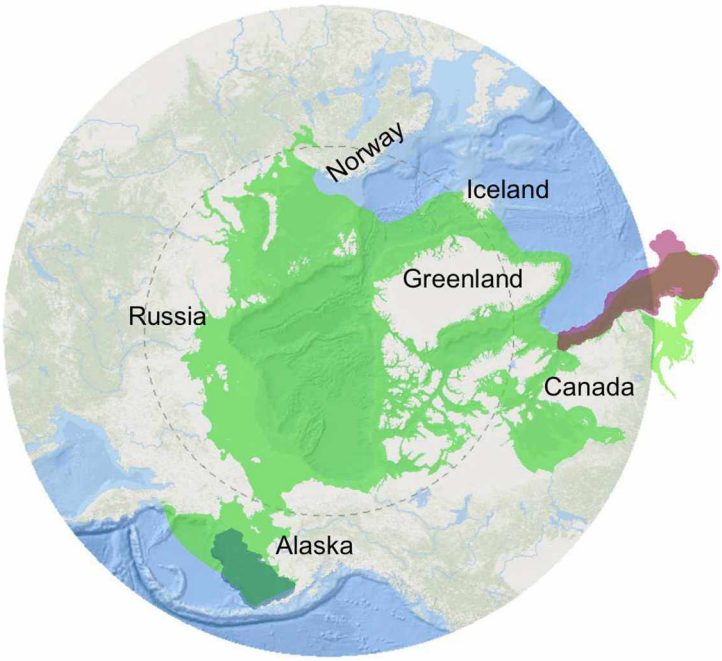

Figure 3.1. Map of the circumpolar Arctic cod distribution (green, based on Mecklenburg 2011 from Thorsteinson 2017) with survey areas highlighted in teal (eastern Bering Sea) and mauve (Newfoundland/Labrador shelf).

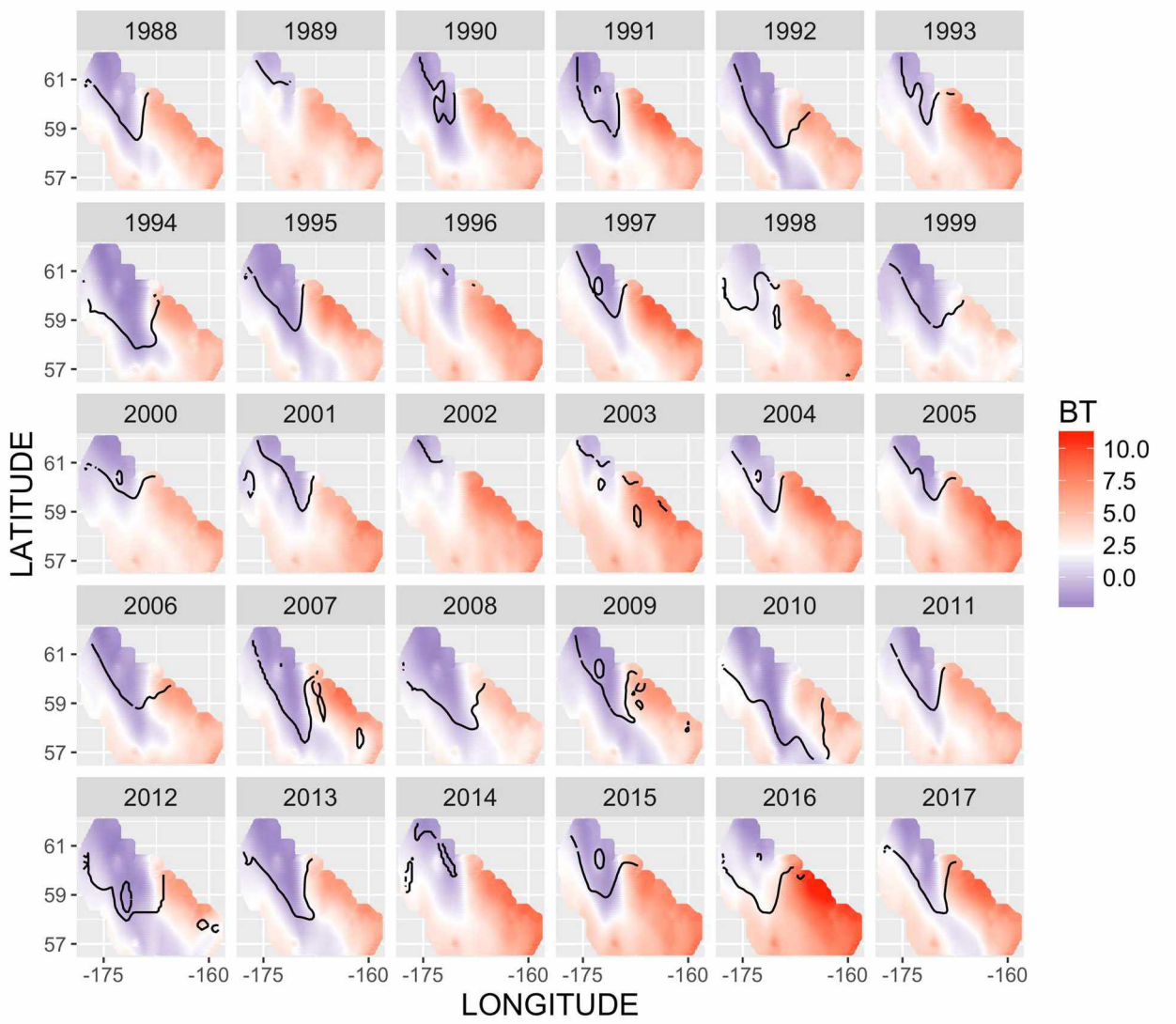

Figure 3.2. Maps of modeled bottom temperatures by year in the Eastern Bering Sea. Blue denotes areas with temperatures below 2 °C (the cold pool) and red denotes temperatures above 2 °C. The black contour lines represent the modeled 20% probability of occurrence for Arctic cod.

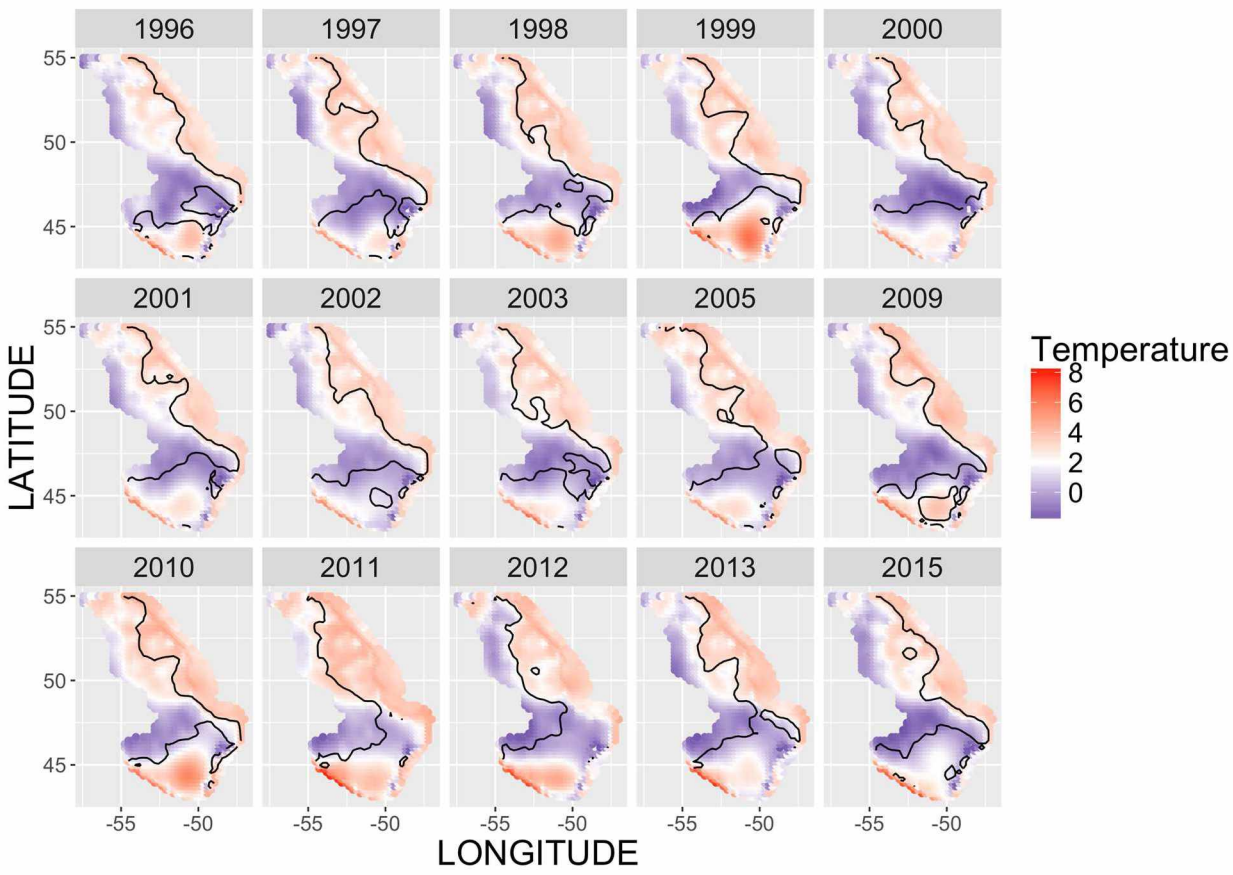

Figure 3.3. Maps of modeled bottom temperatures by year in the Labrador/Newfoundland Region. Blue denotes temperatures below 2 °C and red denotes temperatures above 2 °C. The black contour lines represent the 20% probability of occurrence for Arctic cod.

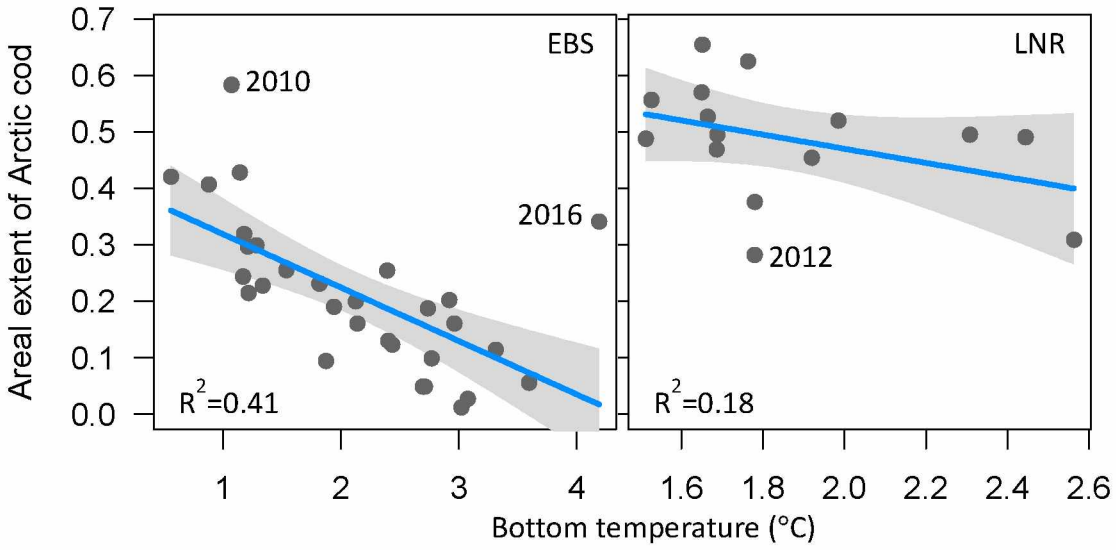

Figure 3.4. Relationships between the fraction of the EBS and LNR survey areas occupied by Arctic cod (>20% probability of occurrence) each year and mean bottom temperature during the survey with linear fits and 95% confidence bands.

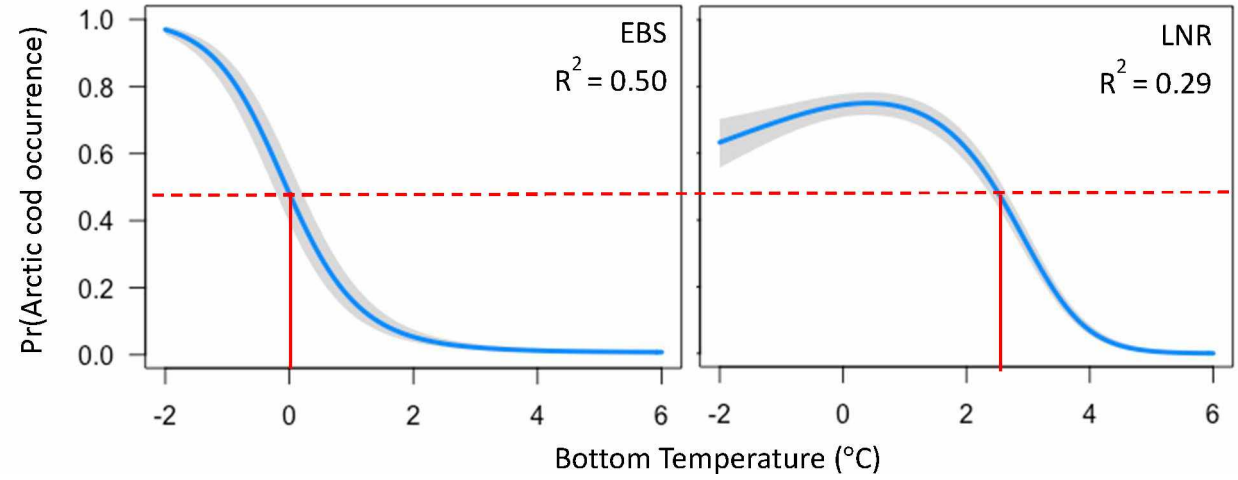

Figure 3.5. Estimated effects of bottom temperature on average probability of occurrence of Arctic cod based on logistic regression of presence/absence on bottom temperature and year by region. Red lines mark the temperatures at which Arctic cod had a 50% probability of being present.

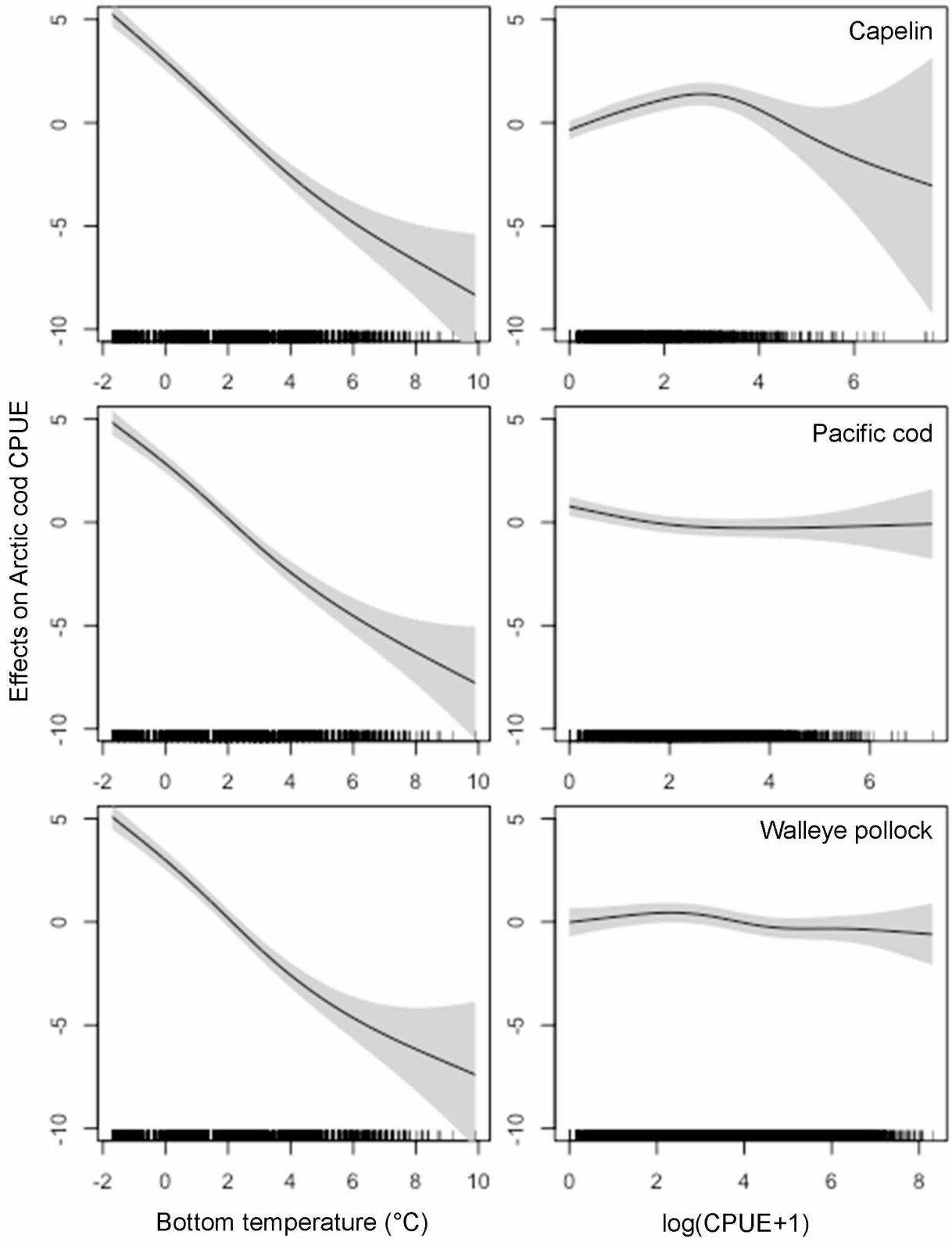

Figure 3.6. Estimated effects of temperature and predator or competitor abundance on Arctic cod CPUE based on best-fit GAMs by species (Table 3.3) for the Eastern Bering Sea with 95% confidence band. Each row depicts the effects from separate models.

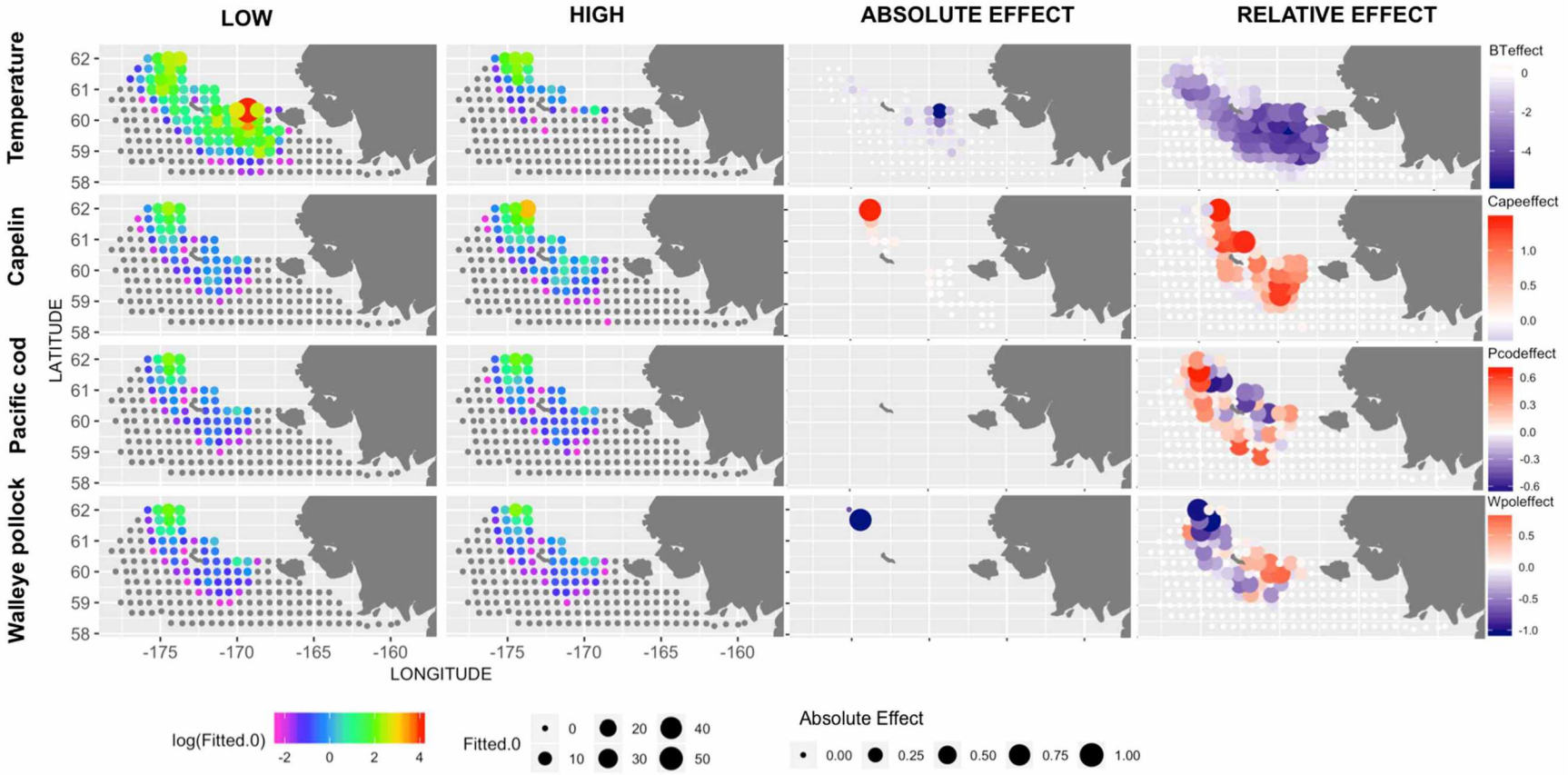

Figure 3.7. Predicted Arctic cod CPUE (left columns) under low and high temperature, capelin, Pacific cod, and walleye pollock scenarios and estimated changes ('effects', right columns) on absolute and log-transformed scale (log-ratios). For the two columns on the left, the size of the circle corresponds to the predicted Arctic cod CPUE and the colors denote log(CPUE) with zero abundances shown in grey. The absolute effects (scaled to range between -1 and 1).

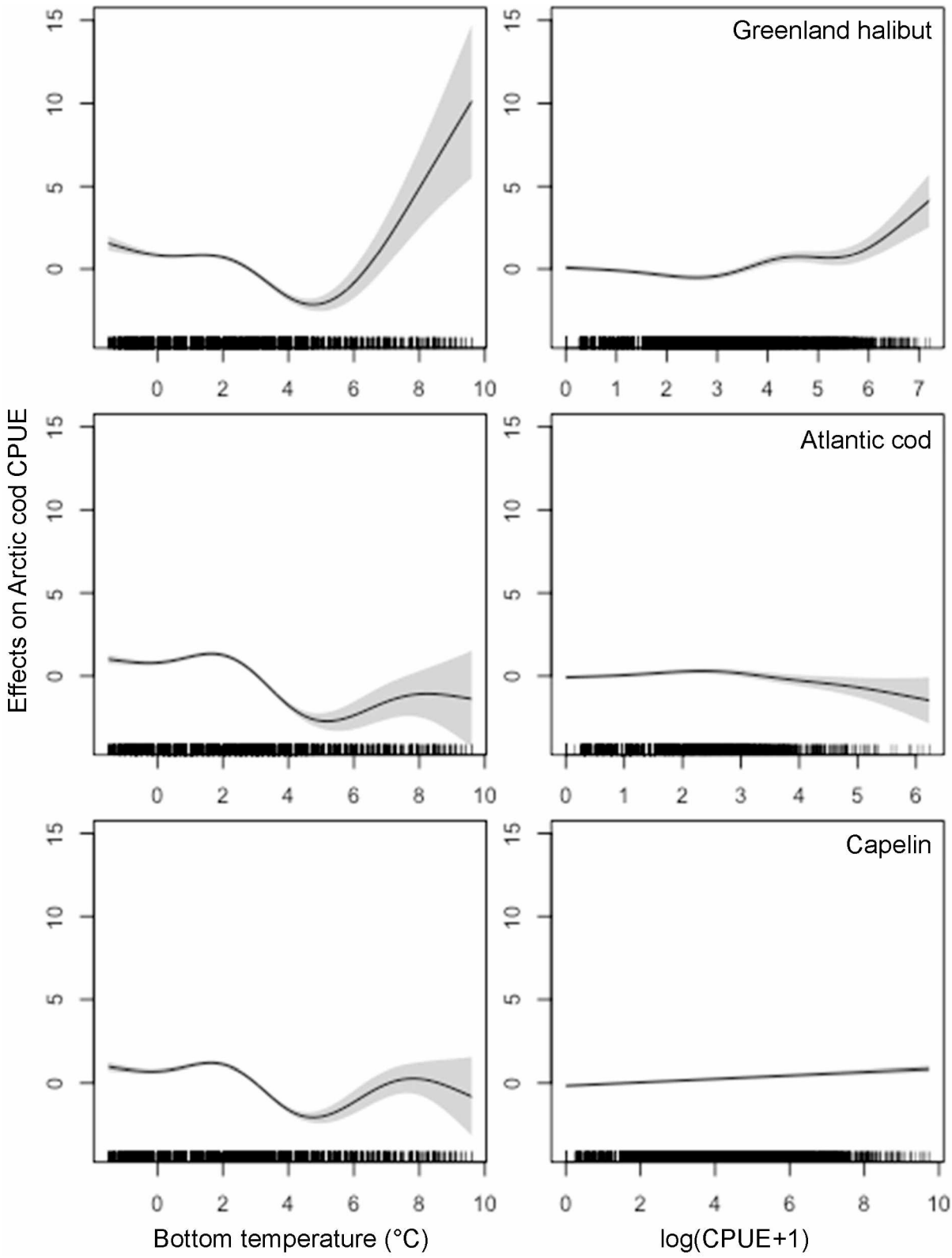

Figure 3.8. Estimated effects of temperature and predator or competitor abundance on Arctic cod CPUE based on best-fit GAMs by species (Table 3.3) for the Labrador Newfoundland Shelf Region with 95% confidence bands.

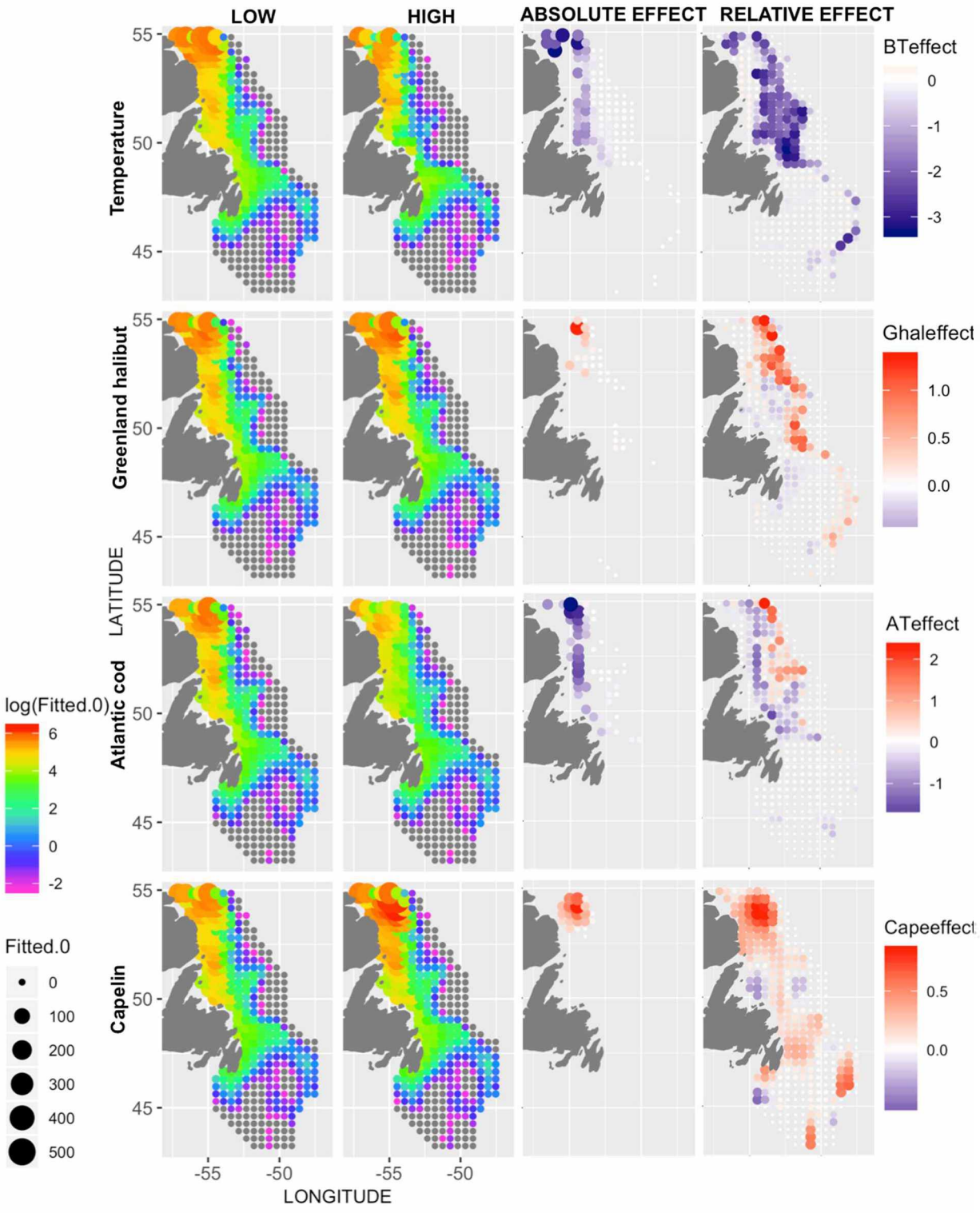

Figure 3.9. Predicted Arctic cod CPUE (left columns) under low and high temperature, Greenland halibut, Atlantic cod and capelin scenarios and estimated absolute and log-transformed scale (log-ratios) in Arctic cod (effects). For the two columns on the left, the size of the circle corresponds to the predicted Arctic cod CPUE and the colors denote log(CPUE) with zero abundances shown in grey. The absolute effects (scaled to range between -1 and 1).

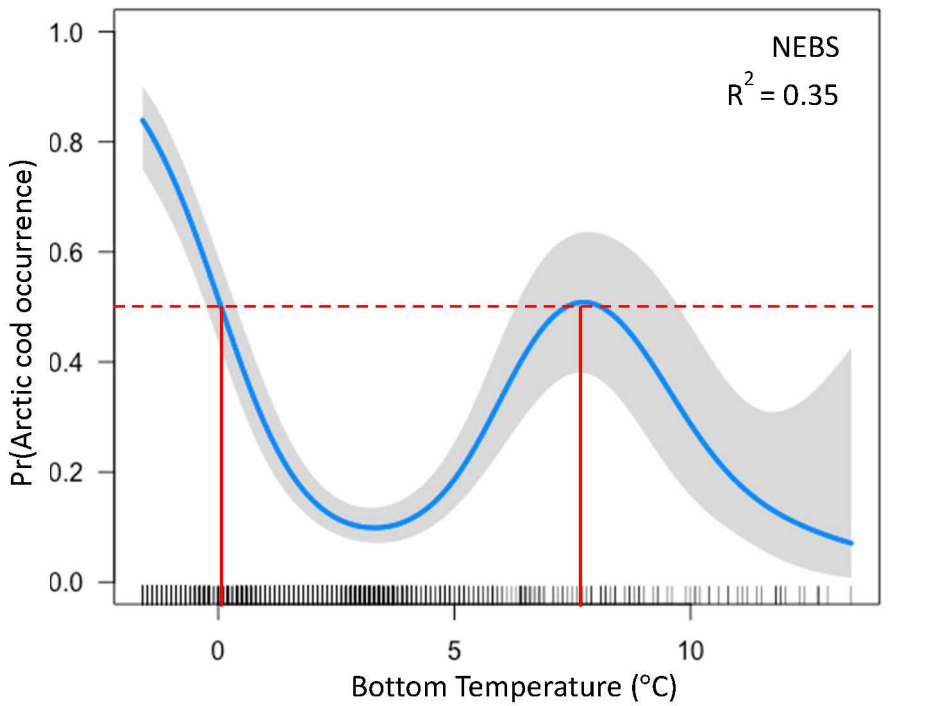

Figure 3.10. Estimated effect of bottom temperature on the probability of occurrence of Arctic cod based on binomial GAM with smooth term for bottom temperature and year-specific intercepts for northern and eastern Bering Sea (NEBS). The red lines mark the temperatures at which Arctic cod had a 50% probability of being present.

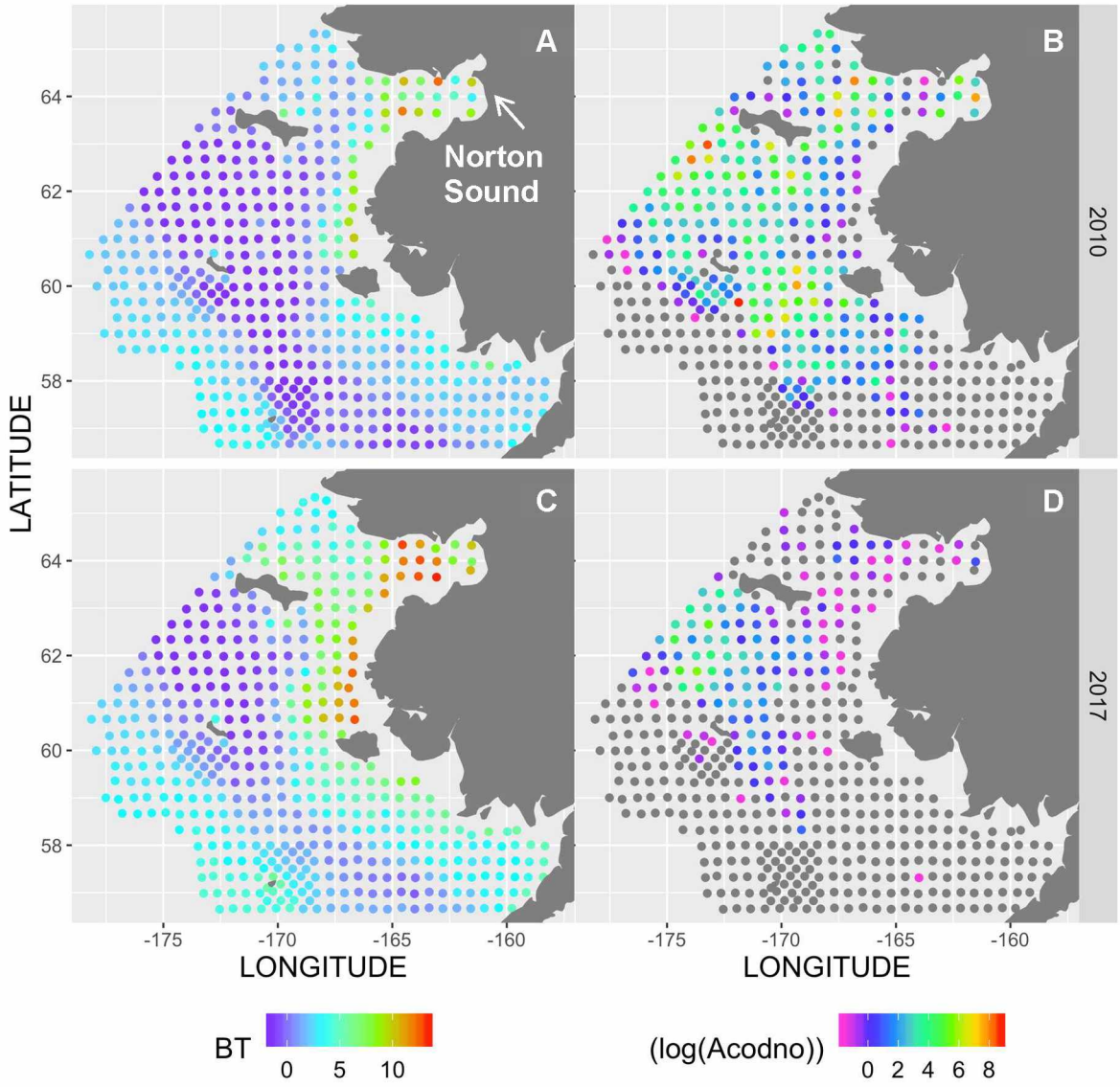

Figure 3.11. Observed bottom temperatures and log(Arctic cod CPUE) from the Northern and Eastern Bering Sea survey in 2010 (A, B) and 2017 (C, D).

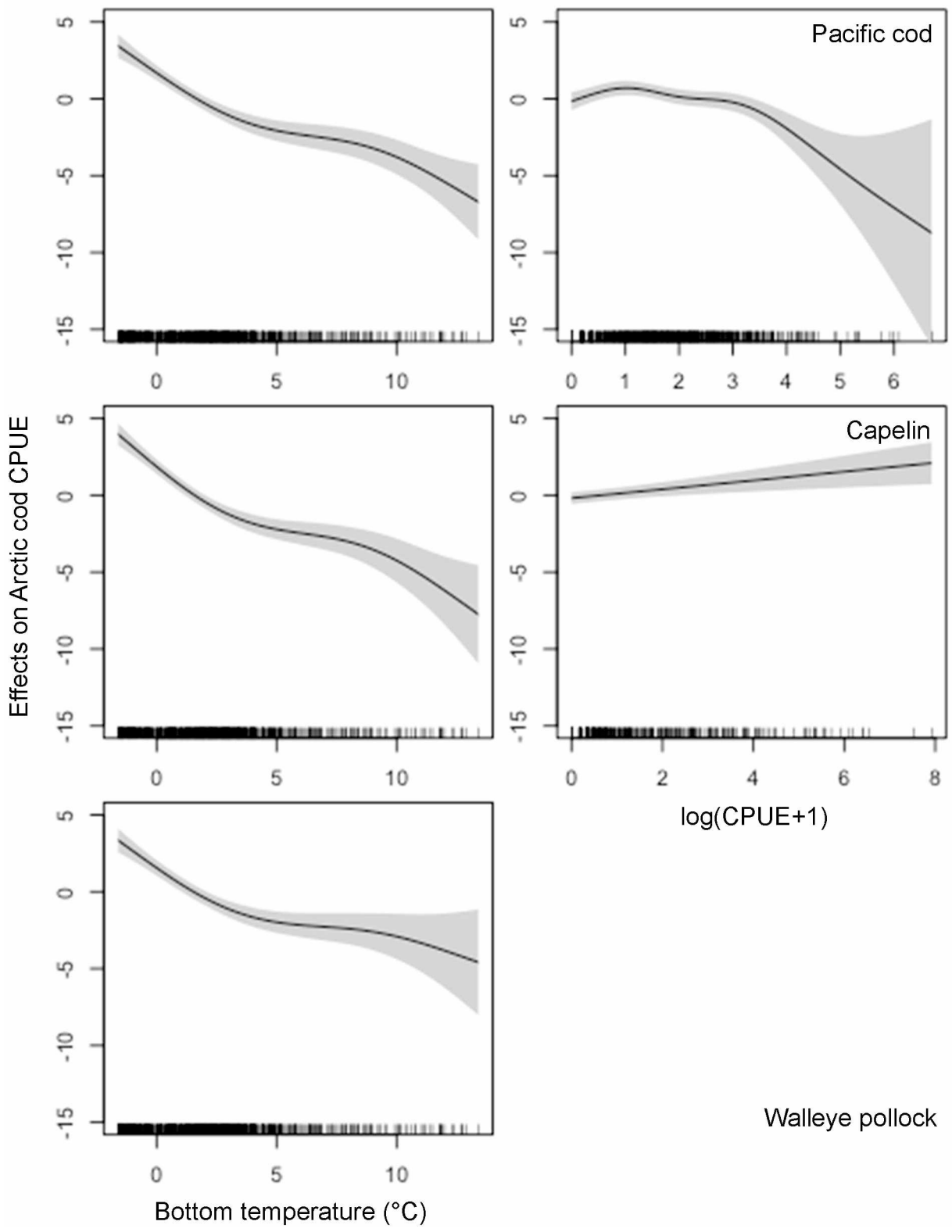

Figure 3.12. Effect of select terms in the best-fit GAMs of Arctic cod CPUE by species from Table 3.4 for the Northern and Eastern Bering Sea. The shaded grey region is the 95% confidence interval.

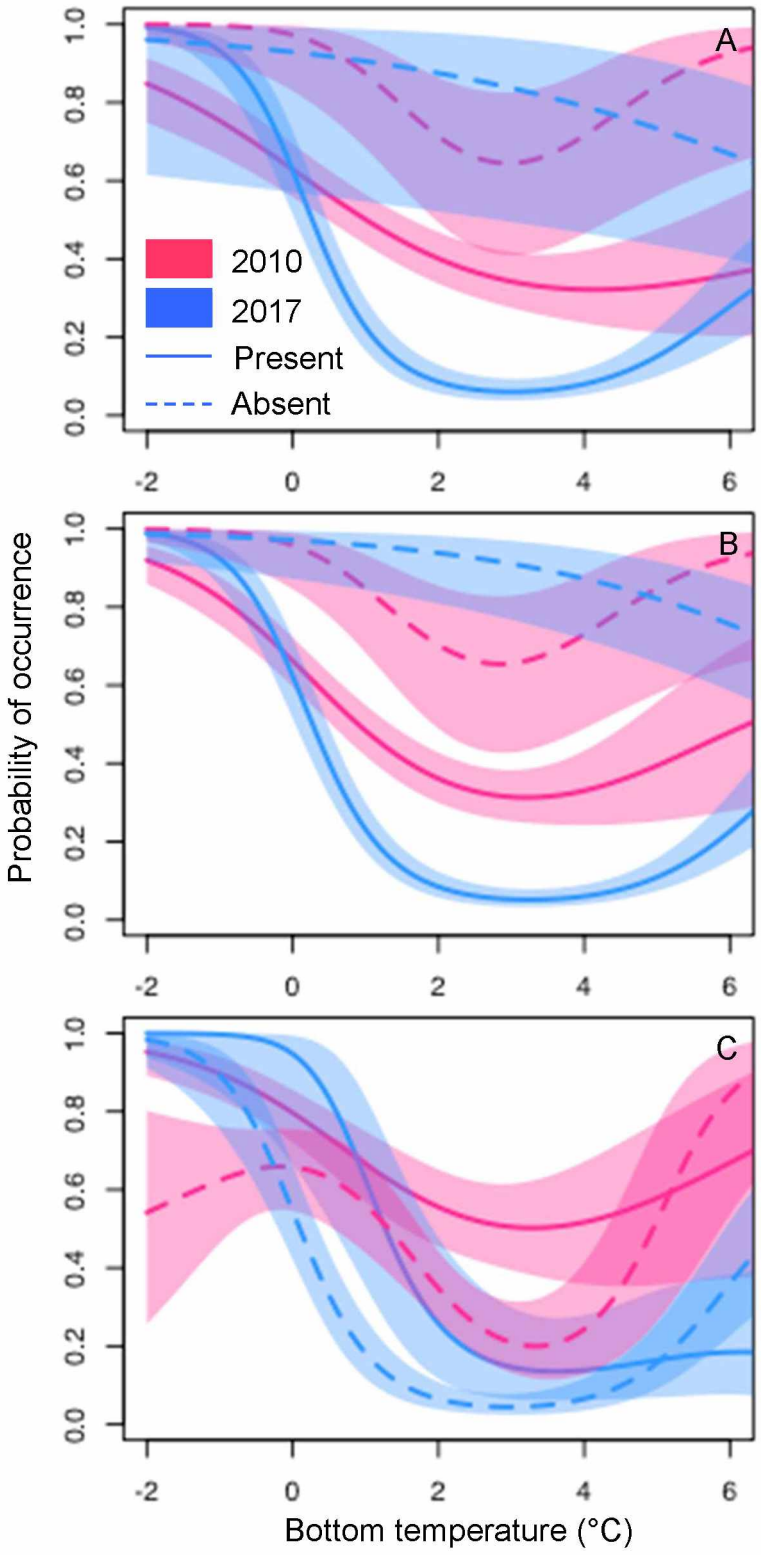

Figure 3.13. Probability of occurrence of Arctic cod as a function of bottom temperature in the presence and absence of Pacific cod (A), walleye pollock (B) and capelin (C) in the northern and eastern Bering Sea during 2010 and 2017 with 95% confidence intervals.

General Conclusions

Overall, this work has advanced our understanding of a key species, Arctic cod, in highly dynamic and rapidly changing Arctic shelf ecosystems. We have gained insight into how this species may respond to climate warming, helping researchers and managers anticipate future changes in diet and distribution. This new information and improved understanding can be used to inform ecosystem mass balance models, stock assessments, oil spill impact studies and species distribution models.

In Chapter 1, I researched the ontogenetic, spatial and temporal variation in trophic roles of Chukchi Sea fishes. I found temporal and spatial variation in the $\delta^{15}N$ and lipid normalized $\delta^{13}C$ ($\delta^{13}C'$) signatures of primary consumers, *Calanus* spp. In both 2012 and 2013, a decline in $\delta^{13}C'$ values from the southwest corner of the survey region to the northeastern Chukchi shelf was observed, while $\delta^{15}N$ values increased to the northeast, although lower values were observed in the far northeastern region in 2013. Spatial and temporal variation in $\delta^{15}N$ and $\delta^{13}C'$ can propagate up through the food web, so fish isotope values were corrected for this baseline variation prior to analysis. Ontogenetic shifts in trophic level and diet were observed for most fish species and these changes tended to vary by water mass. Shifts in foraging habitats with increasing length were observed, as most fish incorporated more benthic prey in their diet as they grew. The exceptions were forage fish species, including walleye pollock, capelin, Pacific sandlance and Arctic cod. Central to the Chukchi Sea food webs was Arctic cod, which was present in all water masses (Pacific-derived Alaska Coastal Water (ACW), Bering-Chukchi Summer Water (BCSW), Chukchi Winter Water (CWW), and melt water (MW). Arctic cod consumed a broad diet, which varied by water mass and year, indicating adaptability and some resilience to ecosystem changes. In 2012, age 1+ Arctic cod in the BCSW fed mainly on pelagic prey, while cod in the MW/CWW incorporated more benthic prey. Age-0 Arctic cod consumed a narrower diet of pelagic lower trophic level prey regardless of water mass and did not occur in the ACW. Similar to age-1+ Arctic cod, the fish community as a whole relied more on pelagic prey in the BCSW, while incorporating more benthic prey in the MW/CWW. The Arctic fish community in the MW/CWW had the smallest isotopic niche space (lowest complexity and trophic diversity), suggesting a limited resource base, but a slightly higher trophic redundancy. Overall, it seems that the Pacific fish community associated with BCSW, which had a broader

resource base, much larger isotopic niche space and higher trophic diversity, will be more resilient in the face of climate change.

In Chapter 2, I used survey information from Arctic Eis and the literature to examine the drivers of distribution and to assess the dynamics and current status of Arctic cod in the Chukchi Sea. Age 1+ Arctic cod are mainly demersal throughout the region and broadly distributed on the shelf over a wide range of temperatures but had relatively low abundances. Temperature was an important driver for both age-0 and age-1+ Arctic cod. The lowest densities of age-1+ cod were observed in the warmest and freshest waters of the ACW, with a steep decline in CPUE when temperatures exceeded 6 °C. In contrast, age-0 fish were concentrated at very high densities in the NE Chukchi Sea primarily in the interface between BCSW and MW/CWW or in BCSW and were more likely to be present in cooler waters. When they were present, the highest CPUEs also occurred at intermediate temperatures (7 °C), which coincided with optimum temperature for growth in laboratory studies (Laurel et al. 2016; Koenker et al. in press). In 2013, the cooler winter waters and melt waters were more widespread, as the warmer ACW did not extend north of 70 °N (Danielson et al. 2017) and age-0 abundance was nearly 3 times larger than in 2012 (De Robertis et al. 2017). The large abundances of age-0 Arctic cod in both 2012 and 2013 were surprising as our estimates of egg production and egg to age-0 survival showed that the observed number of adults in the survey region was likely far too small to account for the number of observed offspring. I suggest that the most likely explanation for this discrepancy is that the biomass of adults observed on the shelf during summer reflects only a fraction of the spawning biomass, implying that adults migrate into the Chukchi Sea to spawn in winter or that most of the young fish are advected from outside the study region. In addition, I provided the first estimates of natural mortality, which appear to be very high compared to other gadids, but are consistent with the importance of Arctic cod as prey for many upper trophic level species in the system. Estimates of vital rates (e.g., natural mortality) can be used in future stock assessments and in biophysical models that form the basis for understanding early life history dynamics and population connectivity and for modeling the effects of oil spills on early life stages. Environmental links to distribution from this study can be used to inform future Essential Fish Habitat models or species distribution models.

In chapter 3, I used time series of groundfish survey data to quantify the variability in distribution and determine which mechanisms (bottom temperature, predators or competitors) are

driving the variability in the Bering Sea and Labrador Newfoundland Shelf Region (LNR). In both regions, Arctic cod occupied more area at lower temperatures and had a higher probability of occurrence, which implies that as temperatures increase the range of Arctic cod is likely to contract. Temperature had a greater effect on Arctic cod distribution than predator or competitor abundance, especially in the eastern Bering Sea (EBS). When I included data from northern and eastern Bering Sea (NEBS) in 2010 and 2017, Arctic cod in NEBS were less likely to occur in warmer waters when either Pacific cod or walleye pollock were present, indicating that range expansions of either subarctic gadid could further restrict the distribution of Arctic cod. Together, the results imply that Arctic cod are likely to be increasingly limited by both warmer temperatures and the northward spread of boreal species that compete with and consume Arctic cod.

This study is particularly timely, as ice conditions and ocean temperatures in the northern Bering Sea and Chukchi Sea have been changing more quickly than anticipated, resulting in expansions of subarctic species, such as walleye pollock and Pacific cod northward and range contractions of the cold-adapted Arctic cod. The 'persistent' cold pool that typically acts as a thermal barrier for subarctic species was nearly absent in the summer of 2018 (R. Lauth NOAA-AFSC, Seattle, pers. comm.). High numbers of walleye pollock and Pacific cod were observed in the 2018 northern Bering Sea groundfish survey, while a total of only seven Arctic cod were caught compared to hundreds in 2010 and 2017 (L. Britt, NOAA-AFSC, Seattle, pers. comm.). While age-1+ Arctic cod occurred throughout the Chukchi Sea, occupying a wider range of temperatures than in the Bering Sea and exhibiting diet adaptability within different water masses, their range during the summer survey season is likely to further contract if warmer waters and subarctic species extend into the Chukchi Sea.

Information from this dissertation can be used to inform management in several ways. Commercial fishing is prohibited in the US Arctic Management Area until there is enough data to support the creation of a sustainable fishery and ensure the sustainability of other ecosystem components (NPFMC 2009). In Chapter 1, we learned from stable isotope signatures that Arctic cod have a broad diet incorporating both benthic and pelagic prey, further bolstering their ecosystem role in transferring energy from pelagic and benthic realms. In addition, trophic levels estimated from 16 fish species can be used in ecosystem mass balance models (e.g., Ecopath). From chapter 2, estimates age-structured biomass, maturity and natural mortality with continued

surveys could inform a more advanced age-structured stock assessment model in a future update of the Arctic Fisheries Management Plan (FMP). Using updated biomass, maturity and natural mortality and the current Arctic FMP stock assessment model (NPFMC 2009), I estimated 765% increase in the MSY from the 2009 estimate of 3,674 mt. for the Chukchi Sea. This increase is mainly due to a much higher natural mortality, which seems plausible given Arctic cod's ecosystem role, and increased estimates of survey biomass. Despite the substantial increase, Arctic cod would be a difficult species to harvest in the Chukchi Sea as their biomass is relatively low and they are spread out over the region. Occasionally, they will form large schools (e.g., Crawford et al. 1996), but those are ephemeral and unpredictable. It should be noted that higher densities of Arctic cod have been observed in the US Beaufort Sea (Rand and Logerwell 2011). Further, in Chapter 3, model results indicated Arctic cod will likely contract their range with an expansion of subarctic gadids. With a warming climate and disappearing cold pool, the summer distribution of subarctic gadids and Arctic cod may shift drastically. Overall, it seems unlikely that the US Chukchi Sea could support an Arctic cod fishery due to climate uncertainty, their relatively low biomass (44,500 mt), low market value (if sold as fishmeal), lack of infrastructure, limited accessibility (short open water season) and the importance of Arctic cod in the ecosystem.

While increasing our knowledge of Arctic cod in Arctic shelf ecosystems, this dissertation also highlighted the need for future studies. There was a sizable mismatch in the relatively low potential egg production of the observed mature Arctic cod in the eastern Chukchi Sea and the high densities of age-0 detected in the acoustic survey. Where do the age-0 Arctic cod originate? Where are Arctic cod spawning? We know very little about early life history survival, region-specific maturity and fecundity, or their distribution outside of the summer season. Also, as Arctic cod are relatively short-lived and can experience sizable population fluctuations (e.g., Datsky 2015), there is need for repeated systematic surveys to assess changes in biomass of Arctic cod and other species of interest (Iken et al. *In Press*).

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